Using a novel methodology to test whether group size affects foraging behaviour in elk.

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Abstract

Group formation is one of the most striking patterns in the natural world. Elk (*Cervus elaphus* and *C. canadensis*) are well known for their social and gregarious nature, but motivations for this behaviour are not fully understood. In particular, how elk perceive and deal with predation risk and modify foraging behaviour as group size changes requires further study.

This thesis begins by describing how group behaviour might add to the security of individuals, using a model that varies adult elk survival with group size. The model might explain why a Lake of the Woods, Ontario, elk population (*C. canadensis manitobensisi*) declined following re-introduction in a translocation program that occurred between 2000 and 2001. The population suffered initially from high levels of predation, possibly due to the predator-naïve nature of the source population from Elk Island National Park, Alberta. A model forcing elk into one of several group sizes, each varying in degree of predation risk describes the predator-naïve nature of introduced elk as contributing to the decline. If individuals adapt to novel predation risks by joining larger groups with higher survival, the population stabilizes and eventually increases.

The majority of this thesis describes anti-predator vigilance levels, estimated both as scanning rates and giving-up densities (GUDs), for captive (farm) elk in groups of 1 through 5, 7, 10, 13, and 17 individuals. GUDs are estimates of the density of food remaining at the end of an experimental feeding bout, in which food mixed with an inert substrate is supplied to individuals free to leave the feeding trays at any time; they have been used to describe a variety of foraging behaviours.

Feeding trials occurred during five study periods in an attempt to determine 1) whether GUDs might serve as a practical, accurate method of assessing risk during foraging with changes in group size, both for focal animals and for the group on average, 2) whether captive elk in larger groups have lower GUDs, 3) whether the presence of dominant animals or the presence of calves in a group might influence foraging behaviours, measured either as GUDs or as time spent vigilant 4) whether spatial position or food density affect scanning and 5) whether elk display a 'many eyes' effect of less time spent vigilant in larger groups.

The GUD methodology proved sensitive enough to detect differences in foraging behaviour in groups varying by just one individual. Elk had lower GUDs in feeding trials with larger groups. Neither dominant foraging behaviour nor the interaction between group size and dominant foraging behaviour had a significant effect on GUDs. GUDs varied significantly with the presence of calves, such that at two group sizes tested, groups with calves had lower GUDs than groups comprising only adults. Calf presence had no significant effect on scanning rate. Food density affected the scanning rate similarly for all group sizes, such that individuals scanned more at the end of a foraging bout when food density was low. The relative spatial position within a group while feeding did not affect scanning rate. Elk displayed a 'many eyes' effect with significantly lower scanning rates in larger groups. It was not possible to attribute the observed group-size effect to an effect of lower predation risk, as both lower predation risk and higher intra-specific competition may have played a role in determining scanning rate. This study, particularly the GUD component, supports the prediction that elk perceive greater risk in smaller groups. Further experimentation and development of this methodology should occur such that it may be used to assess foraging behaviour and decisions in groups of free-ranging ungulates.

Contents

Tables

Figures

Figure Page

Acknowledgments

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Chapter 1: Review of the costs, benefits and motivations associated with animal aggregation.

Elk (*Cervus elaphus* and *C. canadensis*) are well known as a gregarious or social ungulate (Altmann 1952, Geist 1982:145-148). Study of aggregation in mammals has a long history (Ladeveze et al. 2011), and two sets of hypotheses are generally accepted to explain why aggregation occurs in large mammalian herbivores. The first set of hypotheses relates group behaviour to foraging. A first suggestion is that aggregations result when herbivores congregate to exploit certain areas where the nutritional quality and/or availability of food are higher (Kreulen 1975, Western 1975). Where herbivores distribute themselves ideally over a landscape (Fretwell and Lucas 1970), spatial variations in resource availability could be expected to create herbivore aggregations. As examples, spatial variation in resource quality and availability may result from unequal precipitation falling across a region (Western 1975), or from variation in soil nutrient availability (Farley and Fitter 1999). Groups may also be better able than individuals to locate resources in patchy environments (Krause and Ruxton 2002). For example, individuals in a group may benefit from monitoring conspecifics in order to take advantage of the more rewarding patches they have found (Krebs 1974, Lazarus 1978). The 'forage maturation hypothesis' (Fryxell 1991) postulates that aggregation may have evolved because forage plants are maintained in immature, more digestible growth stages by the collective effect of large groups of herbivores (McNaughton 1984, McNaughton 1986). Plants in early phenological stages generally have higher crude protein and lower fibre content (Harkess 1963, Terry and Tilley 1964). Aggregation could in this case even be an adaptive strategy to perpetuate the availability of digestible forage.

The second and perhaps best-recognized set of hypotheses explaining aggregation across diverse taxa invokes an anti-predator strategy (Hamilton 1971, Treherne and Foster 1980, Turner and Pitcher 1986, Cresswell 1994, Fortin et al. 2009). There are many potential anti-predator benefits to larger groups, and these have been treated extensively in the literature (Krause and Ruxton 2002:8-20). The most thoroughly examined are the effects of increasing prey dilution and probability of detecting a predator. Dilution decreases the risk that an individual group member will be captured during a predator attack on a group of prey (Turner and Pitcher 1986, Dehn 1990). When a predator can capture only one prey individual per attack, dilution implies that as group size increases to N individuals each individual's risk of being attacked and captured decreases to 1/N. Dilution, however, is a complex phenomenon. Its strength and the benefit it confers to each individual within a group are affected by group detectability (Treisman 1975, Szep and Barta 1992, Hebblewhite and Pletscher 2002) and the spatial position of individuals within a group (Hamilton 1971), as well as age, sex, condition, posture and behaviour of group members (Bertram 1978, Fitzgibbon 1989, 1990, Fitzgibbon and Fanshawe 1989, Krause and Godin 1996, Childress and Lung 2003, Creel and Winnie 2005). These factors must be considered when interpreting the strength of a dilution effect.

While animals may aggregate to avoid predation, aggregations of prey may be more obvious to a predator and easier to detect than a lone prey item. Turner and Pitcher (1986) argued that the dilution effect should be considered *in tandem* with an avoidance effect in what they termed 'attack abatement.' Their work suggested that a group of prey must not be as detectable as the same number of individuals scattered about a landscape. If a group of prey numbering N individuals is N times more likely to be detected than a lone individual, then there is no advantage to aggregating. Increased detectability with increased group size may result from greater visibility (Krause and Godin 1995) and intensity of olfactory and/or audible cues associated with larger groups of prey (Treisman 1975). Such an attraction effect might completely negate the benefits of larger groups, thus dissolving groups during periods of intense predation risk (Creel and Winnie 2005). Wherever group detectability increases linearly with or more rapidly than group size, prey might be expected to avoid aggregation.

The selfish herd model (Hamilton 1971), based on individual animals' 'domains of danger,' shows that individuals at the periphery of a group occupy inherently riskier and less-favourable positions than conspecifics closer to the centre; this model has received empirical support (Coulson 1968, Fitzgibbon 1990). Hamilton (1971) also suggested that during times of vulnerability or predator presence prey groups would clump more tightly. Support for this prediction has been provided in several studies encompassing a variety of prey taxa (Spieler 2003).

Further supporting the notion that dilution is not a simple rule of mathematical security for an individual in a larger group are several examples where individual characteristics predispose an animal to being selected for attack over one of its group mates. Wolves (*Canis lupus*) have been shown to favour attacks on elk of a certain age and sex (Creel and Winnie 2005), and Fitzgibbon (1990) observed cheetahs (*Acinonyx jubatus*) target and kill more male than female gazelles (*Gazella thomsoni*). The potential for predator targeting must be weighed against the strength of a dilution effect (Bednekoff and Lima 1998). While empirical studies have produced mixed results, predators have generally been shown to target non-vigilant or less vigilant prey (Fitzgibbon 1989, Cresswell et al. 2003). Spatial position and predator targeting may both cause variations in the relative benefit that an individual gains from group membership. Such variations are often due to *per capita* differences in vigilance.

A group-size effect centered on anti-predator vigilance was first modeled by Pulliam (1973), and has since received significant theoretical as well as empirical attention (Lima 1995a, 1995b, Dehn 1990). The model predicted that with increasing group size, individuals benefit from a higher number of conspecifics scanning their surroundings for threats. ‘Many eyes’ mean that an approaching threat is more likely to be detected than by any single set of eyes, and any additional individual can add to the group’s total vigilance, while allowing other group members to relax their time spent vigilant and spend more time feeding. This ‘many-eyes’ effect remains one of the most reported trends in ecological literature (Cresswell 1994, Liley and Creel 2007). However, with increases in group size, individual predation risk decreases through the effects of dilution, detection and confusion. Therefore, as group size increases, the individual may decrease its commitment to scanning without increasing its risk of predation, regardless of the corporate vigilance in the group (Roberts 1996). Generally, the risk of predation for individuals in a group varies according to predator attack rate, the probability of detecting a predator given the group is attacked, and the probability of escaping given the likelihood of an attack. Regardless of the mechanisms or predictions, it is generally accepted that these three factors will vary with group size.

Probability of detection of a predator, related to the overall vigilance of a group, is correlated with factors other than group size. Group composition may play an important role in determining overall vigilance levels (Laundre et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003). Females with young may exhibit greater vigilance levels and often do not reduce their vigilance as would be expected. Liley and Creel (2007) observed female elk in groups with higher proportions of calves to have higher vigilance levels. Lipetz and Bekoff (1982) showed that vigilance among female pronghorn antelope (*Antilocapra americana*) was greater in groups with calves. Higher vigilance may also be related to social or physical position within a group, with peripheral group members having higher levels of vigilance than their counterparts at the centre of a group (Krause and Ruxton 2002). Distance to the nearest perceived threat can impact vigilance levels, even if the threat is not immediate. Liley and Creel (2007) documented vigilance above baseline levels in elk when wolves were present, with increasing levels as wolves moved closer. Group vigilance is generally higher as distance to cover as a means of concealment increases, and is higher in open areas compared to areas with protective cover (Elgar 1989, Hernandez and Laundre 2005). Presence of and distance to escape impediments have also been shown to affect vigilance levels (Creel and Winnie 2005, Halofsky and Ripple 2008). Food density is perhaps the greatest confounding variable in predicting vigilance (Elgar 1989). Intra-group competition, social status, sex, age, time of day, ambient temperature and individual foraging ability have all been shown to affect the relationship between vigilance and group size (Elgar 1989).

Group behaviour has benefits both as a foraging strategy and as an anti-predator strategy. These benefits though, are not without costs. A thorough knowledge of both costs and benefits, and how they interact to shape animal behaviour, will help a researcher better understand a given study system.

Chapter 2: Exploration of the potential population effects of different aggregation strategies in elk introduced to Ontario.

While several hypotheses explain why aggregation occurs in social animals, perhaps the best recognized suggests that forming groups is an anti-predator strategy (Hamilton 1971, Treherne and Foster 1980, Turner and Pitcher 1986, Cresswell 1994, Fortin et al. 2009). The potential anti-predator benefits to larger groups, i.e. the ways to explain 'safety in numbers,' are many, and they have been treated extensively in the literature (Krause and Ruxton 2002:8-20). The most thoroughly examined are the effects of increasing prey dilution and probability of detecting a predator. Dilution generally implies that each animal within a group is advantaged as group size increases because there is a lower probability that any one individual will be attacked (Hamilton 1971). Group vigilance, on the other hand, increases the odds that an approaching predator will be detected before attacking a group (Pulliam 1973). As group size increases, there are more sets of eyes scanning for predators and each individual can decrease its own commitment to vigilance, all the while allowing the corporate vigilance of the group to increase. The effects of increasing dilution and detection have been described in the context of anti-predator strategies in many social ungulates (Dehn 1990, Scheel 1993, Bednekoff and Ritter 1994). For example, for several species of antelope (*Raphicerus campestris, Ourebia ourebi, Redunca arundinum, Syncerus caffer, Aepyceros melampus, Damaliscus lunatus, Connochaetes taurinus, Hippotragus niger*), increases in group size correspond to decreased time invested in vigilance by each group member, while the total time scanning by the group increases (Underwood 1982).

Elk (*Cervus elaphus* and *C. canadensis*) are known for forming aggregations. Although this behaviour may persist where predators are absent, it has usually been described in areas where large carnivores are present. For example, in Yellowstone National Park (YNP), elk devote more time to vigilance in the presence of wolves (*Canis lupus*) than nearby populations in Rocky Mountain National Park, a predator-free environment (Wolff and Van Horn 2003). Elk in habitats that had been wolf-free for fifty years increased vigilance significantly just one year after wolf re-introduction to YNP (Laundre et al. 2001). Elk now increase baseline vigilance in response to the appearance of wolves on the YNP landscape, suggesting that this behaviour is a way of mitigating predation risk. Furthermore, forming groups may be a means for elk to manage predation risk. Dehn (1990) used data on Rocky Mountain elk (*Cervus canadensis nelsoni*) in the Mist Valley, Alberta, to test several models of elk anti-predator behaviour and concluded that group vigilance was important in predator avoidance at small group sizes (<10 animals), but that for larger group sizes, dilution was the likely benefit to forming groups. Hebblewhite and Pletscher (2002) similarly showed for elk in Banff National Park that small groups were detected less often by wolves than larger groups, while larger groups provided security to the individual via dilution.

This chapter explores how elk introduced into Ontario, Canada, during 1999-2001 may have variably adjusted to a new experience of predation risk by dispersing or by forming smaller and larger groups. The source population for the re-introduction was Elk Island National Park, Alberta, a predator-free environment (Frair et al. 2007). Four locations were chosen for re-introduction. The first three are Bancroft/North Hastings (BNH), Nipissing/French River (NFR) and the Lake Huron North Shore (LHNS). Late-winter aerial surveys have indicated that the elk populations in these areas have been increasing since re-introduction, with individual groups as large as 53 (Ontario Ministry of Natural Resources, unpubl. report). Elk introduced into the fourth location, near Lake of the Woods (LOW) in Northwestern Ontario, have been the slowest to establish and may face exceptionally high levels of predation; as an example, 22% of mortalities following release of elk into the LOW area were attributed to wolf predation (Ontario Ministry of Natural Resources 2009). The LOW population is believed to have recently stabilized, and groups of up to ten individuals were observed in the area during a 2011 late-winter, aerial survey (Ontario Ministry of Natural Resources, unpubl. report).

This chapter introduces three scenarios for LOW elk, modeled using demographic data during this population's early establishment: one in which social behaviour is forced and the population increases due to an assumption of 'safety in numbers,' a second where failing to adopt this behaviour explains an initial population decline, but later aggregation leads to population increase, and a third where social behaviour is not adopted, and the population declines following release.

Lake of the Woods elk:

Over the winters of 1999-2000 and 2000-2001, 104 Manitoban elk [*Cervus elaphus manitobensis* (Polzeihn et al. 1998)], transported by truck from Elk Island National Park, were soft-released into the area of Cameron Lake Road in Northwestern Ontario, approximately 25 km northeast of the town of Nestor Falls. The introduced population became known as the Lake of the Woods (LOW) elk. Shortly after release, 10 adult male and 12 adult female elk emigrated permanently from the area, with the majority of dispersal to the south (McIntosh 2003). Known mortalities were 25% for each of the first two years following release, with 15/60 and 11/44 animals dying in 2000 and 2001, respectively (Rosatte et al. 2007). While it was estimated that the entire population numbered 85 animals in a survey on June 1, 2002, a recent estimate suggests only 35-45 animals remain within 20 km of the original release site, with a few single individuals and small groups within a 100-km radius of the release site (Ontario Ministry of Natural Resources 2009). Population estimates for the other three release areas are higher than the LOW estimate, although it should be noted that more elk were released into two of the remaining three release areas [120 in Bancroft/North Hastings area and 172 in the Nipissing/French River area (Rosatte et al. 2007)]. Maximum group sizes of 53 individuals have been observed in both the Bancroft/North Hastings (BNH) and Nipissing/French River (NFR) populations, while the largest group in the Lake Huron North Shore (LHNS) area was 21 (Ontario Ministry of Natural Resources, unpubl. report). Many smaller groups sizes have been reported in all four areas.

The modeling approach:

A model was developed using Microsoft Excel that incorporated data on release numbers, herd composition, mortality and emigration of elk introduced to the LOW area from 2000-2001. The model relied on two key assumptions: 1) elk living in larger groups were subject to inherently lower risk of predation and 2) elk are behaviourally flexible animals capable of responding to variations in predation risk on the scale of years. Three scenarios, incorporating one or both of these assumptions were tested. In a first scenario for this model, all elk formed groups of three or larger (3+) each year after 2001. In a second, groups of 1, 2 and 3+ elk were formed initially, but behaviour leading to single (dispersing) elk was eliminated by the third model-year, and behaviour leading to groups of just two elk (pairs) were eliminated by the sixth model-year. The attempt in the second scenario was to match how elk behaviour might change over time when a new population is exposed to predation risk and increasingly adopts anti-predator behaviour. In the third scenario, groups of 1, 2 and 3+ formed initially, and persisted each year after 2001. Survival probabilities of 0.5, 0.7 and 0.9 were applied to group sizes of 1, 2 and 3+, respectively, for all animals > 1 year old, drawn from published rates (White 1985). A survival probability of 0.33 was applied to calves (< 1 year-old elk) each year, approximated from a published rate (Boyce 1989:57). Male elk were not included except as calves that forced their mothers into groups of 3+. The actual group size distribution was irrelevant, as survival was assumed to be the same for adults in any group in the 3+ category.

A total of 32 adult (> 2 year-old) females, 5 yearling (1-2 year-old) females, and 5 female and 6 male calves (< 1 year old) were known to have survived from release to the end of 2001 (McIntosh 2003). These animals were carried into a first model-year assuming their survival at least to the spring of 2002. In the first scenario, they were assigned in each year and in all cases to groups of 3+. In the second scenario, surviving elk in 2002 were assigned each year to different group size classes according to the following rules: all calves and a number of adult females equal to the number of calves (both male and female) were assigned to groups of 3+. The remaining pool of adults was divided into three equal groups, with one third going into each of the three group size categories until 2004. After 2004 and until 2007, the pool of adult females was divided into two, half going into each of only the two larger group size categories. The pool of yearling females was always divided into two, half going into each of the two larger group size categories until 2007. By 2007, the first two scenarios were identical and all animals of all ages were assigned to groups of 3+. In the third scenario, surviving elk in 2002 were assigned every following year to group size classes according to the same rules as for the second scenario in its first two years.

Yearlings to survive winter were moved into an adult cohort without contributing to recruitment. Recruitment was calculated based on the number of adult females to survive each winter. Adult females in each group size were assumed to have a pregnancy rate of 0.88 (Boyce 1989: 51). As twins are very rare in elk populations (Johnson 1951, Taber et al. 1982), only single calves were born to any pregnant female. As even sex ratios are typical of elk (Angstman and Gaab 1950, Johnson 1951, Boyce 1989:51), and taking into account the calf survival rate, only 16.5% of calves born survived to contribute to the female yearling population. It was assumed that no emigration occurred after the first two years following release. Formulae representative of the modeling rules were entered and applied to the initial population data in a Microsoft Excel spreadsheet for all three scenarios from 2002 through 2015.

Results and discussion:

In the first scenario, the female population increased from 37 in 2002 to 52 by 2015 (Fig. 1). In the second scenario, the population initially declined to a low point of 32 in 2005. The population then stabilized and increased by 2008, to reach 41 females by 2015. In the third scenario, the population declined from 37 animals in 2002 to 21 females by 2015. The purpose of this model is not to generate a current estimate of the LOW elk population. Rather, if living in larger groups reduces predation, the model illustrates the potential importance of group formation and how differential survival among groups of different sizes might affect population growth in elk.

The first scenario, showing an increase one year after release, seems unrealistic, both according to surveys of the LOW elk and according to results of translocations elsewhere. In Alberta, Canada, where elk naïve to predation risk were translocated into areas of high predation risk, first-year survival rates were 1.9-2.2 times lower than counterparts having previous experience with predators (Frair et al. 2007). Post-release data on elk in the LOW area indicate six elk were

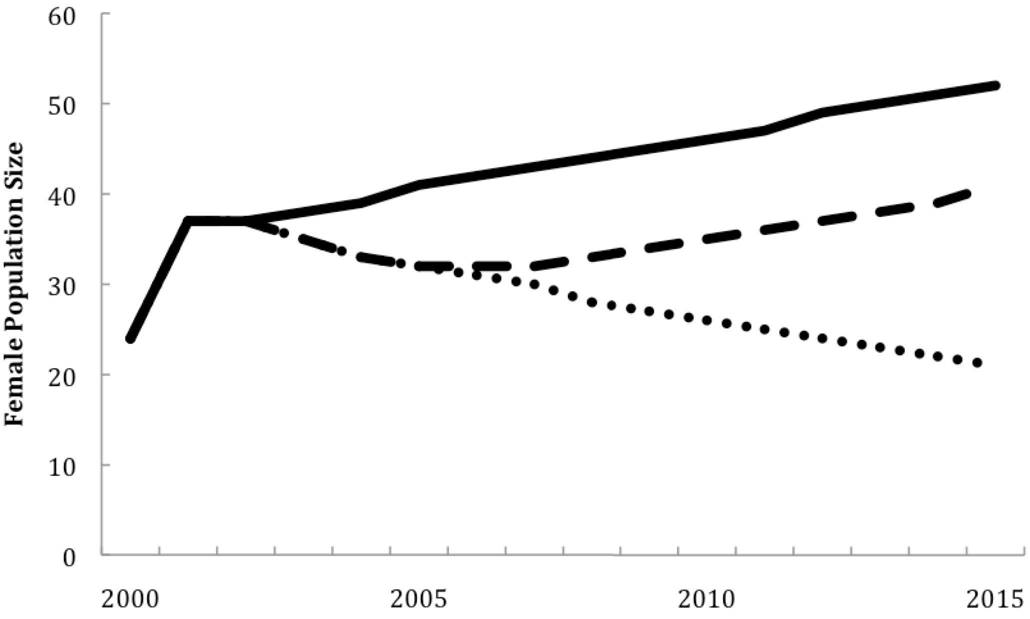

FIG. 1. Population models for elk introduced in 2000/2001 to the Lake of the Woods area of Ontario according to three scenarios where survival probabilities of 0.5, 0.7 and 0.9 were applied to group sizes of 1, 2 and 3+ respectively. If all animals are assigned to groups of 3+, the population increases (solid line). If part of the population occurs initially in smaller group sizes of 1 and 2, the population initially decreases, stabilizes after the removal of single animal behaviour, and then increases after the removal of paired animal behaviour (dashed line). If part of the population occurs persistently in smaller group sizes of 1 and 2, the population declines (dotted line).

killed by wolves and another ten were shot in the first two years following re-introduction (Rosatte et al. 2007), making it unlikely that the population began to increase immediately following release.

More reasonable is that in their first few years in a predator-rich environment, predator-naïve elk invested little into anti-predator behaviours such as group formation and vigilance. Small groups and single animals would be poor at coping with the novel predation risk posed by wolves. Such a scenario may have occurred in the NFR elk release area, where elk failed to avoid direct and indirect sources of predation risk (Kittle et al. 2008). In that area, losses due to wolf predation in the first four years after re-introduction ranged from 19% - 29%, the highest for any of the four elk release areas (Rosatte et al. 2007). Nevertheless, predator-naïve elk, as well as other ungulates, have been shown to respond with increased anti-predator behaviours upon exposure to novel sources of predation in as little as a single generation (Berger et al. 2001, Laundre et al. 2001). This is the second modeled scenario.

While both increased vigilance and dilution effects can contribute to group security, it is unlikely that dilution contributed significantly to the security of elk in the LOW area. Aggregation in elk is understood to be density dependent (Hebblewhite and Pletscher 2002), and with only 104 elk introduced successfully to the LOW area (Rosatte et al. 2007), initial group sizes were likely all small. At small sizes, individual vigilance provides far more security than would a dilution effect (Dehn 1990), and time invested by individuals in vigilance is time not spent foraging. McIntosh (2003) observed elk introduced to the LOW area showed high levels of use of red pine (*Pinus resinosa*)/white pine (*Pinus strobus*) forests that had been harvested 5-15 years prior to the study. Dewar (2006) also reported that elk in the LOW area were closely associated with recent forest harvesting activities. Disturbed areas provide large volumes of desirable forage, including graminoids, forbs and shrubs (Skovlin et al. 2002). However, forest openings also provide better visibility, making anti-predator vigilance more effective. Indeed, aggregation in open areas is typical of elk, and has been cited as both a foraging and predator avoidance strategy (Creel and Winnie 2005, Liley and Creel 2007). While studies by McIntosh (2003) and Dewar (2006) both interpreted use of forest openings in early successional stages as a foraging response, the potential for use of such areas as a means of predator avoidance should also be considered, as direct and indirect predation risk and the use of anti-predator strategies can have important fitness consequences to the individual and ultimately influence population growth (Brown 1999, Brown et al. 1999, Laundre et al. 2001, Fortin et al. 2004). As anti-predator behaviours, including aggregation into larger groups, developed in LOW elk, the population may have been able to stabilize, increase, and consequently form increasingly larger groups with higher corporate vigilance. Indeed, the current consensus is that the LOW population is no longer in decline (Ontario Ministry of Natural Resources, unpubl. report).

The third scenario, with the population in steady decline, suggests relatively inflexible behaviour in elk, and is not supported by literature. Frair et al. (2007) reported that one year after translocation, elk naïve to predators had survival rates comparable to resident elk accustomed to predators. Ungulates are behaviourally flexible animals, capable of adjusting levels of anti-predator behaviours, such as vigilance, in response to variations in predation risk (Brown et al 1999). Several studies of a variety of ungulate species support this idea (Underwood 1982, Lagory 1986, Scheel 1993, Bednekoff and Ritter 1994, Creel et al. 2008), as do studies of a large range of avian, mammalian and piscine predator-prey systems, reviewed by Lima and Dill (1990).

Chapter 3: Use of giving-up densities to assess foraging behaviour in aggregations of elk (*Cervus canadensis*).

Animal aggregation is one of the most striking patterns in the natural world. One hypothesis suggests that aggregation serves to mitigate the predation risk of individuals within a group (Hamilton 1971, Krause and Ruxton 2002:8-9, 2002:13-18). While foraging, animals often raise their heads to scan their surroundings. As the size of an aggregation increases, there are more animals scanning for potential predators (i.e., vigilant), increasing the likelihood that a threat will be detected with sufficient time to take evasive action (Pulliam 1973, Lazarus 1978, Godin et al. 1988). Increases in group size also provide security to animals foraging in a group through the dilution of risk – the familiar concept of 'safety in numbers' (Hamilton 1971, Foster and Treherne 1981).

Vigilance, or scanning rate, has often been used as a metric for determining the relative risk that gregarious animals perceive during foraging (Cresswell 1994, Laundre et al. 2001, Wolff and Van Horn 2003). In the context of evaluating predation risk in animals foraging as a group, higher scanning rates are generally taken to indicate greater perception of risk (Scheel 1993, Laundre et al. 2001, Fernandez et al. 2003, Dias 2006, Creel et al. 2008).

A second method of assessing costs and risks in foraging is by use of 'giving-up densities' (GUDs; Brown 1988). Foraging theory predicts that an animal should maximize its investment in a foraging activity as long as the net gain per unit of food acquired exceeds the loss (MacArthur and Pianka 1966). When foraging optimally in an environment where resources are distributed heterogeneously in patches, an individual is expected to feed in a patch until the energy gained by foraging just balances its metabolic, predation risk, and missed-opportunity costs (Brown 1988), as in the following equation:

$$\mathbf{QHR = C + P + MOC} \quad \text{(Equation 1)}$$

where H is the forager's instantaneous rate of intake, C is the metabolic cost of foraging, P is the cost of managing predation risk while feeding, and MOC represents the missed-opportunity cost incurred by the forager when it chooses to feed in a particular patch instead of partaking in some other activity, including reproduction, maintenance, or feeding in another patch. Where an abundance of high quality foraging patches exists (i.e., where MOCs are high), Equation 1 predicts that a forager should abandon a feeding patch at a relatively high rate of harvest.

It is difficult to measure a forager's rate of harvest the moment it abandons a foraging patch. It is easier and more conventional to measure the density of food left once a forager has left a patch. An experimental design to allow this measure typically involves installing artificial feeding trays as feeding 'patches,' where the metabolic cost of foraging, C, is controlled over a feeding bout by mixing food items in an inert substrate. The density of food remaining in the substrate at the end of the bout, the GUD, is used as an approximation of a forager's quitting harvest rate (Brown 1988) i.e.,

$$\mathbf{GUD = QHR = C + P + MOC} \quad \text{(Equation 2)}$$

Foragers treat predation risk as a cost (Kotler 1984, Brown et al. 1988) and an individual forager should choose to abandon a riskier patch at a higher rate of harvest, leaving behind a higher GUD than it would in a safer patch. Higher costs of predation risk, P, could, therefore, lower the quality of a foraging patch by decreasing the resources that a forager feels safe in extracting before it chooses to abandon the patch. However, high GUDs are not necessarily evidence for high values of P, as they may also be indicative of high MOCs, either due to high environmental quality in the surrounding habitat or, in the case of an experiment, specifics related to the experimental design. For example, to test an effect of increase in group size on GUDs, providing more feeding trays to additional foragers may increase MOCs if some foragers eat more slowly and others (e.g., dominants) see partially consumed trays increasingly as missed opportunities.

It is worth noting here that competition may also contribute to the cost of foraging. For example, if aggressive interactions between conspecifics lead to greater metabolic costs than the simple cost of foraging, then it should be expected that foragers would decrease their foraging time (Mitchell et al. 1990). Similarly, competition might result in a reduction in available resource density. If such a reduction occurs, then search times increase, thus decreasing the marginal benefit of foraging (Mitchell et al. 1990). This again would lead to a reduction in foraging time.

Experimental GUDs have been used to assess a host of questions related to foraging behaviour, including evaluation of response to riskiness of different habitat patches (Brown et al. 1988, Kotler et al. 1994, Altendorf et al. 2001, Orrock et al. 2004), decisions on foraging in open patches versus seeking thermal cover (Rieucau et al. 2007, Rieucau et al. 2009), measurement of changes in physiological costs between seasons (Whelan and Jedlicka 2007), response to variations in patch and habitat quality (Hochman and Kotler 2006, Olsson and Molokwu 2007), and as behavioural indicators of population density and temporal variations in resource availability (Morris and Mukherjee 2007). Such studies have focused on categorical variables, such as different microhabitat types. GUD experiments have also usually concentrated on unknown foragers (i.e., one individual indistinguishable from others that may have fed from the same tray). GUDs have rarely, if ever, been used as a means of assessing continuous variables, such as changes in perception of risk in prey groups of a range of sizes. But if individuals can be tracked and they each experience higher security by foraging in larger groups, through any of the group benefits described above, then they might exploit patches to a lower instantaneous rate of harvest with increasing group size.

As mentioned, most GUD studies measure giving-up densities of unknown foragers and can draw conclusions based only on the amount of food left behind. Here, we applied the GUD methodology in a novel fashion, by observing the GUD trial taking place. Having the ability to watch GUDs occur allowed us the opportunity to view changes in MOCs as food was depleted in a tray. Experimentation with GUDs and measurements of time spent vigilant were undertaken in marked captive elk. Specifically, the tests were 1) whether GUDs might serve as a practical, accurate method of assessing risk with changes in group size, both for focal animals and for the group on average 2) whether elk in larger groups have lower GUDs, 3) whether the presence of dominant animals or the presence of calves in a group might influence foraging behaviours, measured either as GUDs or as time spent vigilant, 4) whether spatial position or food density affect scanning and 5) whether elk display a ‘many eyes’ effect of less time spent vigilant in larger groups.

Materials and Methods:

Study Area.- Egli’s Sheep Farm Limited, Minnitaki, Ontario, is roughly 20 km west of Dryden, Ontario. The property is subdivided into six, fenced, open-field paddocks ranging in size from 4 to 8 ha. To the north, the property is bordered by Trans-Canada Highway 17, and to the east, south and west by a mixed forest of trembling aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*). An active rail line, approximately 500 m away, parallels the southern edge of the property.

Data collection took place between January 12 and April 1, 2011. Daytime temperatures ranged from -29 ^{O}C to 4 ^{O}C with a mean on test days of -11.1 ^{O}C. Snow depth ranged from approximately 0.5 m at the start of the study to about 0.9 m in mid-March and decreased thereafter, although snow depth in small areas within paddocks exceeded 1.0 m. Throughout the study, frequent snowfalls occurred.

Study Animals. - Twenty-six Manitoban elk (*Cervus canadensis manitobensis*), descendant of elk sourced from Elk Island National Park, were subjects of the study. Half the animals were females ranging in age from 3 to 9 years. Two yearling (year-old) females and 11 calves (young-of-the-year) were also included. Despite living in a semi-controlled environment, elk in the study displayed large flight zones, an avoidance of humans, farm equipment, vehicles, and dogs that approached paddocks. Each animal wore a unique ear tag and was uniquely recognizable. Study animals had *ad libitum* access to dried grass and generally received no other rations, except during the last study period, when, according to seasonal farm care practices, a grain feed (approximately 0.75 kg per animal) was provided immediately following the daily trials.

Feeding trays were wooden boxes with a top opening approximately 53 cm X 23 cm, and a depth of approximately 20 cm (Fig. 2). Each tray was assigned a unique number spray painted on the outside of all four vertical surfaces for identification at distances >100 m. Trays were filled with a mixture of 500 g dried, livestock-grade alfalfa pellets (AlfaTech Livestock Feeds, Manitoba, Canada) and 300 pieces of 2.5 cm long, 2.5 cm diameter black polyvinyl chloride (PVC) tube. This proportion of alfalfa pellets and piping was used in all trials and provided a depletable matrix with diminishing returns, with feeding animals incurring progressively greater feeding costs with each piece of food that was removed. The opening of each tray was overlaid with two pieces of heavy wire to create three, equal-size openings of 0.23 m by 0.18 m in each tray (Fig. 2). The wire prevented spillage of the alfalfa/piping mixture from the tray during feeding bouts. Animals were allowed to feed from trays during a seven-day period immediately preceding the study to ensure familiarity with the trays.

FIG. 2. Photograph of a feeding tray used in the study. Trays were wooden boxes with a top opening approximately 53 cm X 23 cm, and a depth of approximately 20 cm.

Feeding Trials. – The study was divided into five periods, each lasting approximately two weeks. During each period, elk were randomly assigned to groups of various sizes and only one group was kept in any paddock. Five paddocks allowed up to five groups to be observed during one period. Group sizes ranged from 1 through 5, 7, 10, 13 and 17. Only groups > 3 included calves, which were not part of the feeding trials; groups > 7 always included calves, due to a limited pool of elk to draw from for the larger groups. At least one day was allowed after groups were formed and before feeding trials were started to habituate animals to their new setting.

Feeding trial areas of approximately 150 m^2 were cleared of snow in each paddock for the duration of the study. Feeding trials took place between 8:30 a.m. EST and 1:00 p.m. EST in a group order randomly chosen each day. Trays were arranged in the trial areas either in one straight line, with a separation of approximately 3 m between trays (Fig. 3a), or in a series of similar straight lines, each line separated from the next by approximately 3 m (Fig. 3b). The number of trays available in a feeding area usually equaled the number of animals in the group. However, for groups of 13 and 17, only 10 trays were set out. This was acceptable as groups of these sizes contained several dominant animals that would have left behind multiple GUDs even if a number of trays equal to group size had been set out. At such large group sizes, it would have been difficult to set out all trays before some feeding began, possibly biasing results.

Elk were observed from a parked vehicle at distances ranging from 75 – 100 m. One observer, A. Moreira, was present during all trials. A 10-60 power spotting scope (Swarovski) or 10-32 power binoculars (Burris) were used to identify feeding elk, based on a combination of unique ‘bite marks’ in their coats and from ear tags, where legible. The identity of the last elk to feed from each tray was recorded and the GUD for the tray was assigned to this individual. While feeding, elk groups were also filmed using a digital video recorder (Digital Sony HandyCam) mounted on a collapsible tripod. Once all individuals in a group had completed feeding bouts (defined as the departure of the last elk feeding from any tray), contents of all trays were collected and the remaining alfalfa was separated from the piping. Alfalfa pellets were kept below freezing in a sealed plastic bag to discourage water absorption, and were later oven-dried to a constant mass at approximately 90 ^{o}C. It was unlikely that any correction to final dried pellet mass would have been necessary due to moisture content of alfalfa from the supplier. The product was guaranteed to contain less than 3% moisture by mass and was stored in sealed bags in a very dry area prior to use. In instances when one individual was the last to feed from multiple trays, the GUDs for all such trays were combined and averaged for that individual. In such instances, the size of missed-opportunity costs was compared between the individuals using multiple trays, labeled dominant animals, and the other individuals in the same group, labeled subordinates.

Video Analysis of Vigilance Behaviour. - A scan sampling procedure (Wolff and Van Horn 2003) was used to assess the average amount of time spent vigilant by individuals in the same group during each feeding bout. The first ten minutes of a foraging bout were selected in the video record, and a scan of each group member (excluding calves) was made at 15 s intervals. Individuals were classified as scanning (head held above shoulder height in an alert posture with ears pointed forward), feeding, walking, standing, socializing or grooming. Aggression was considered socializing. The total number of each behaviour occurring during a foraging bout was tallied and then divided by the total number of behaviours recorded during the bout. This yielded a proportion of scanning behaviour for the group during the ten minute sampling period. Scanning rate was the proportion of time spent scanning.

To determine whether food density impacted vigilance levels, the first and last two minutes of a group's foraging bout were selected and behaviours were recorded as described above. It was assumed that the greatest amount of food would be present during the first two minutes of a foraging bout, and the lowest amount of food would be present during the last two minutes of the bout. It should be noted that all trials were conducted with the same initial mass of alfalfa pellet i.e.: 500 g.

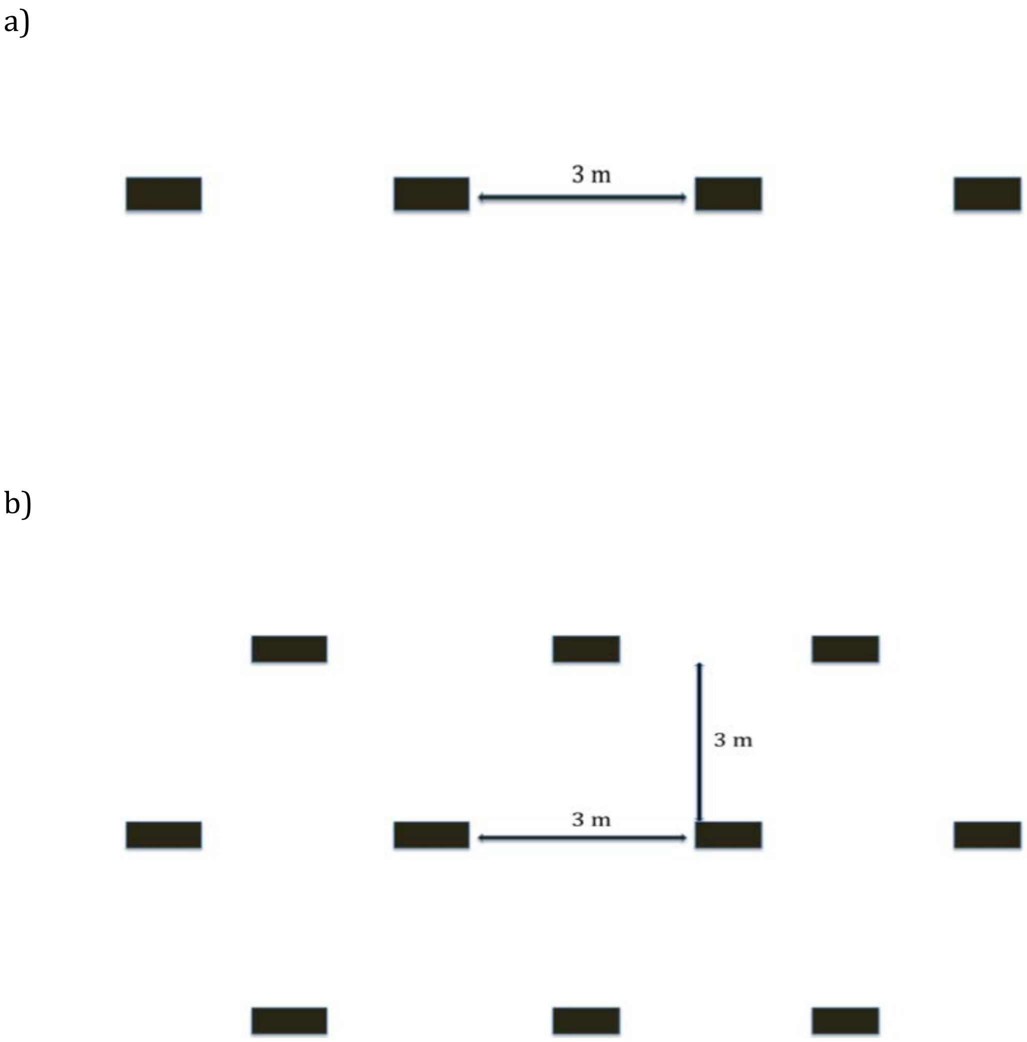

FIG. 3. Two general arrangements of feeding trays used in the study. The trays for group sizes 1 through 7 were arranged in a straight line, spaced 3 m apart (a). The trays for groups of 10, 13 and 17 were arranged in a series of lines. Trays in each line were spaced 3 m apart, while lines of trays were 3 m from one another (b).

For group sizes > 3, differences in scanning rate among individuals feeding at inner and outer trays, potentially safer and riskier feeding positions, respectively, were compared using a focal animal sampling procedure (Altmann 1974). For this analysis, a four-minute sampling bout was selected, during which one individual remained and fed at an inner trays, while a second fed consistently at one of the outermost trays. In instances where such a four-minute period was not available, a minimum of ten consecutive, simultaneous behaviours were recorded for the two focal animals being observed. Behaviours were recorded as above.

Data Analysis.- Repeated-measures ANOVA was used to test for an effect of the day of the feeding trial on the first dependent variable, GUDs, during each test period. During the period of the first feeding trials, only one group of 10 was tested. Since group size represented the between-subject effect in the repeated measures ANOVA used, and there was only a single group size tested during this period, a test for an effect of group size was not available during this period. During all other periods, effect of group size was tested. Behaviours across periods were not assumed to vary significantly. Individual elk were used as the experimental units (replicates), allowing for the repeated-measures design. Linear regression modeled the effects of group size and dominant foraging behaviour (use of multiple trays by one individual) and tested for an interaction effect of group size and dominant foraging behaviour on GUDs: $\text{LogGUD} = \beta_o + \beta_1\text{GroupSize} + \beta_2\text{Dominant}$ $\beta_3\text{GroupSize*Dominant}$ (Model 1). Because the presence of calves was not independent of group size, two-way ANOVA was used to compare GUDs in groups of 4 and 7 elk tested in different periods with and without calves. For all analyses, GUDs were logarithmically transformed to correct for a right skew, thus normalizing the data and satisfying the assumption of homoscedasticity, as typical for GUD experiments (Brown 1988). GUDs were also log-transformed for the linear regression to illustrate the orders of magnitude in differences between larger and smaller group sizes.

The second dependent variable, scanning rate, was also log-transformed prior to analysis to satisfy assumptions of normality and homoscedasticity and to present large differences clearly. Linear regression was used to model effects of group size on scanning rate: LogScanning = $\beta_0 + \beta_1$GroupSize (Model 2). As for GUDs, two-way ANOVA was used to compare scanning rate for groups of 4 and 7, with and without calves. Repeated-measures ANOVA tested for differences in scanning rate during periods of high (start of a foraging bout) and low food densities (end of a foraging bout), with the two food densities acting as separate treatments over time. The scanning rate for individuals at inner and outer trays was similarly compared using repeated-measures ANOVA. The experimental unit in all analyses of scanning rate was the group, since individuals were not recognizable during film review; consequently it was not possible to test for an effect of daily variation in scanning rate. Statistical Package for Social Sciences version 18.0 was used for all analyses.

Results:

GUDs.- For four of the five periods, no effect of the day of the trial on GUDs was detected (Table 1). A significant and negative effect of increasing group size on GUDs was detected during three of the four periods for which a repeated-measures test was possible. These were the last three periods of the study. During the period February 9 – February 25, group size also had a significant effect on GUDs, while the effect of day also became significant.

TABLE 1. Effect of group size and variation by day on giving-up density (GUD: amount of food left in a patch once a forager quits feeding there) in five study periods. In all study periods except the first, where group size was not tested, group size had a significant effect on GUDs. Variation by day only had a significant effect on GUDs during the second study period.

Date	Period	Number of Days Tested	Group Sizes	Effects Tested	F	*p*
January 24- February 3	1	4	10	Day	3.23	0.10
February 8- February 28	2	4	2, 3, 4, 17	Day	30.80	<0.01
				Day*GroupSize	6.54	<0.01
				GroupSize	7.59	0.02
March 2 – March 14	3	3	2, 4, 5, 13	Day	0.22	0.80
				Day*GroupSize	1.25	0.34
				GroupSize	9.89	0.01
March 16- March 24	4	4	1, 4, 7	Day	1.37	0.29
				Day*GroupSize	1.05	0.43
				GroupSize	81.92	<0.01
March 27- April 1	5	4	1, 7	Day	0.49	0.69
				Day*GroupSize	0.43	0.73
				GroupSize	33.40	<0.01

GUDs decreased significantly with group size (Fig. 4). The effect of group size did not decrease in a linear fashion. The difference in GUD between group sizes one and two was predicted as 12.3% (37.154-31.696) while the difference predicted between group sizes 16 and 17 was only 0.02% (5.047-4.426). Neither dominant foraging behaviour, nor the interaction between group size and dominant foraging behaviour had significant effects (Model 1: Table 2). GUDs varied significantly with the presence of calves at the two group sizes compared (groups of 4: F = 17.1, $p < 0.01$; groups of 7: F = 111.2, $p < 0.01$); the groups with calves had lower GUDs than the groups comprising only adults at the two group sizes tested.

TABLE 2.- Table 2. Effects of group size (GPSZ) and dominant foraging behaviour (DOM) on GUDs (Model 1) and effect of group size on scanning (Model 2). Group size is the only significant effect.

Model 1: $LogGUD=\beta_0+\beta_1GPSZ+\beta_2DOM+\beta_3GPDOM$

Regression	Adj. R^2 =.278	df = 3	$p < 0.01$	Int. = 1.702
Factors	β	Std. Err.	t	*p*
GPSZ	-0.063	0.007	-9.56	< 0.01
DOM	-0.273	0.181	-1.50	0.13
GPDOM	-0.005	0.908	-0.11	0.90

Model 2: $LogVig=\beta_0+\beta_1GPSZ$

Regresion	Adj. R^2=.605	df=1	p <0.01	Int. = -0.721
Factors	β	Std. Err.	t	*p*
GPSZ	-0.066	0.005	12.00	<0.01

Vigilance. - Time spent scanning during ten-minute sampling bouts decreased significantly with group size (Model 2: Table 2; Fig. 5). The presence of calves in groups of 4 and 7 had no significant effect on scanning rate at the group sizes tested (groups of 4: F = 1.41, p = 0.24; groups of 7: F = 0.36, p = 0.55). Food density affected scanning rate, which was higher at the end of a foraging bout when foraging patches had been depleted and food density had decreased (F = 7.92, p < 0.01; Fig. 6). The relative position of the tray did not affect the scanning rate of feeding animals (F = 0.01, p = 0.95).

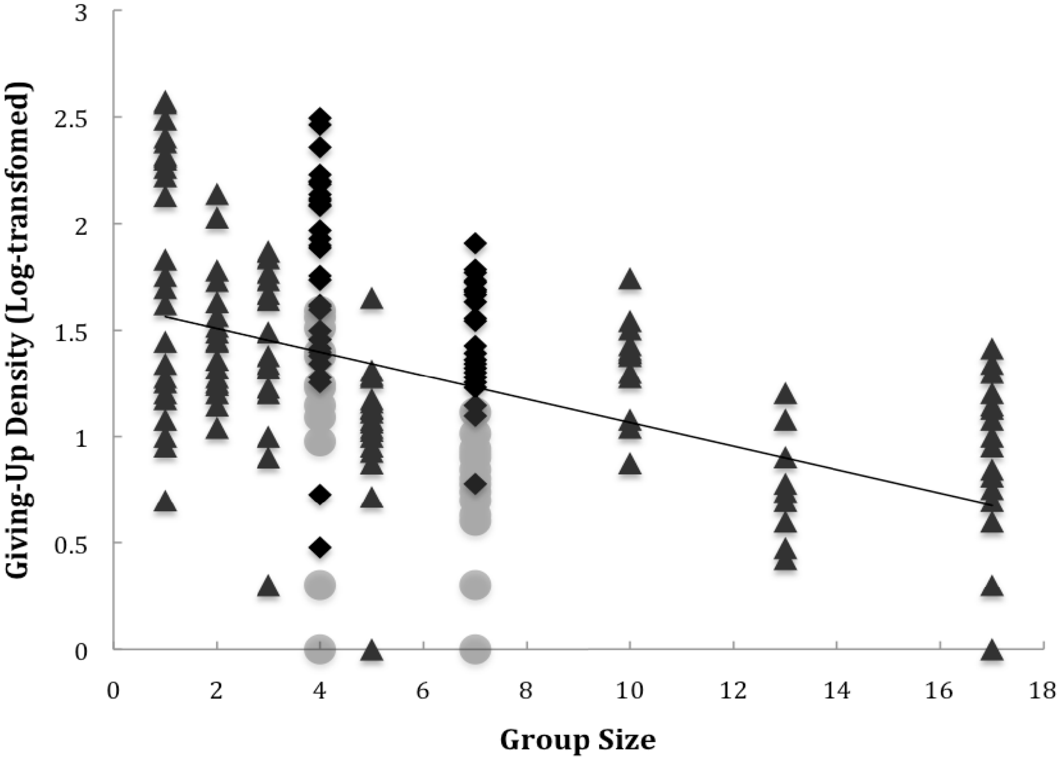

FIG. 4. Giving-up densities (GUDs) of elk according to group size. Circles and diamonds represent groups with and without calves respectively, in groups of four and seven elk. Triangles represent GUDs for all group sizes where a test for an effect of calf presence was unavailable. GUDs decreased significantly with group size (Adjusted R^2 = 0.278, β = -0.063, p < 0.01, S.E. = 0.007).

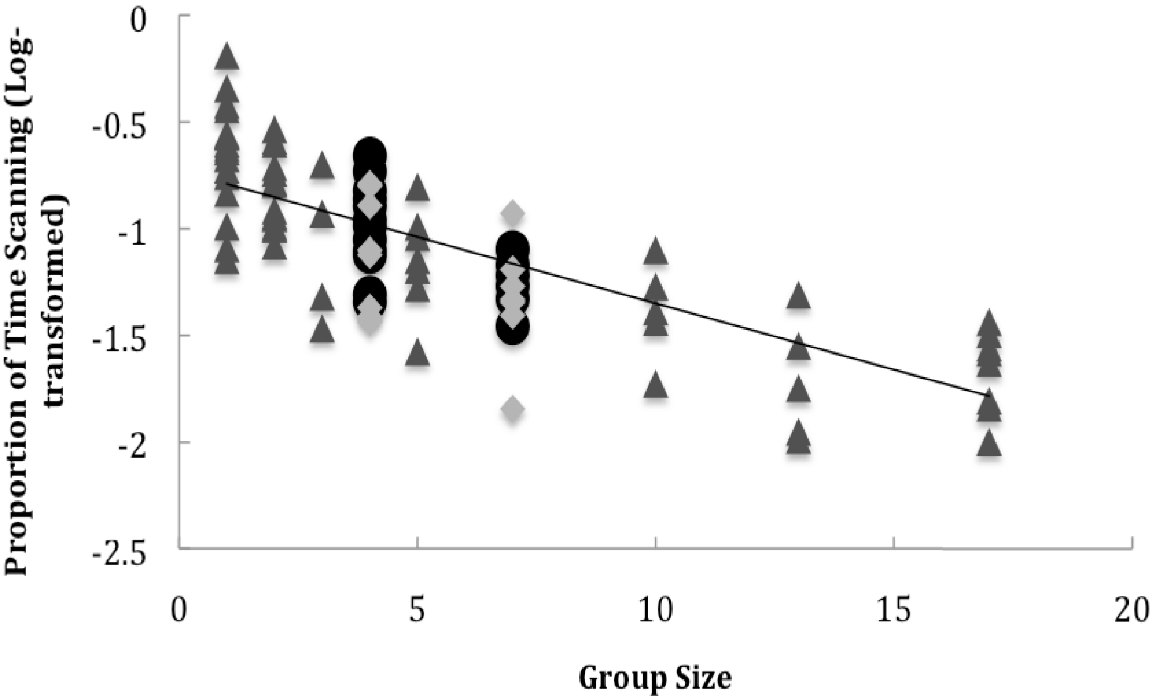

FIG. 5.- Time spent scanning by elk during 10-min sampling periods. Diamonds and circles represent scanning times for groups with and without calves respectively, at group sizes four and seven. Triangles represent scanning times for all groups where no test for an effect of calf presence on scanning was available. Scanning decreased significantly with group size (Adjusted $R^2 = 0.605$, $\beta = -0.066$, $p < 0.01$, S.E. = 0.005).

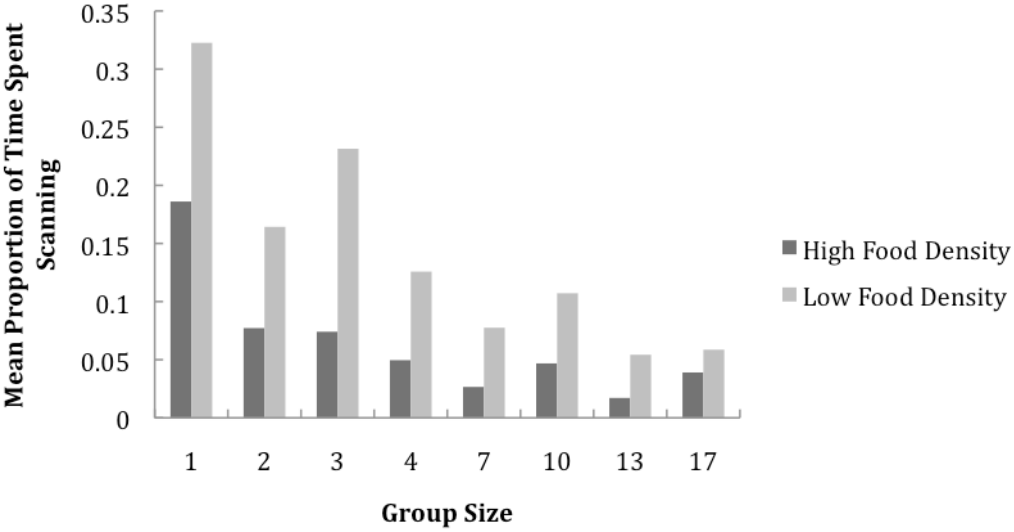

FIG. 6.- Time spent scanning by elk according to food density. Elk spent significantly more time scanning at times of low food density (end of a foraging bout) than at times of high food density (start of a foraging bout) (F = 7.92, $p < 0.01$). All feeding trials were conducted with an initial mass of alfalfa pellets of 500 g.

Discussion:

As expected if larger group size is associated with lower predation risk, GUDs were lower in feeding trials with larger groups. Except in one of the study periods, the day on which a feeding trial took place had no significant effect on GUDs. Given the assumption that group size and therefore predation risk remained constant within each study period, the daily variation in GUDs in the anomalous period must have been due to changes in the metabolic cost of foraging. For example, thermoregulatory costs can significantly affect GUDs, causing them to vary among more and less thermally-favourable feeding locations (Kilpatrick 2003). The period with a significant daily variation in GUDs included the coldest and warmest recorded daily temperatures of the entire study (-29 ^{0}C and 4 ^{0}C respectively), resulting in the greatest degree of variation in temperature of any of the study periods.

Although it was assumed that variation in cost of predation would be due to variations in predation risk, risk may result from factors other than predation (Krause and Ruxton 2002: 41, Morris 2009). There existed the potential for increased intra-specific competition in larger groups to be associated with higher risk in feeding and thereby to influence GUDs. Aggressive behaviour from dominant animals could have been perceived as a risk, causing subordinates to abandon feeding prematurely and leave behind higher GUDs. There is no reason to believe this situation occurred in the feeding trials, however, since analysis revealed no effect of dominant feeding behaviour on GUDs. In this study, scanning rate also increased when food density decreased. Prothero et al. (1979) noted that elk are well-known for maintaining dominance hierarchies and Harper et al. (1967) observed dominant individuals in groups of elk to be alert to their group mates finding food; these individuals would displace their subordinates to appropriate their feeding patches. Although dominant individuals should have perceived such opportunities more often than subordinates, and therefore used more feeding trays, higher GUDs were not left behind by individuals feeding on more than one tray. However, the possibility of GUDs increasing with higher competition above the range of group sizes tested here should not be ruled out.

The decrease of GUDs with group size followed an exponential relationship. In particular, larger differences occur in the GUDs of single individuals *versus* small groups than additional differences in GUDs as new members are added to a group. It is likely that even at very large group sizes, the perception of risk will never decrease to zero. Although dilution decreases the likelihood that any one individual will be killed during a single, successful predatory attack, each individual might be subjected to many attacks over the course of its life, suggesting that maintaining at least a certain minimum level of apprehension is important to survival (Dehn 1990).

Individuals in groups with calves had lower GUDs, contrary to findings elsewhere that female elk with calves perceive greater levels of risk (Wolff and Van Horn 2003). In the farm setting, perhaps separation from their calves agitated mothers and resulted in slightly higher GUDs than if their young had been present. Nevertheless, such an effect did not mask the group size effect that was detected.

While GUDs did decrease with group size, group size was confounded with period. Due to logistical issues, it was not possible to replicate the host of group sizes tested over all periods. However, day within a period had no effect in four of the five periods tested, suggesting perhaps that periods did not differ tremendously. Christianson and Creel (2007) found that time of winter, early, middle and late, had only small effects on elk winter foraging. If GUDs did vary by period, then snow depth (Christianson and Creel 2007), ambient temperature

(Kilpatrick 2003), moon phase (Kie et al. 1991), and perhaps even progression of pregnancy in adult females may have affected foraging behaviour between periods.

Pronounced decreases in scanning with increases in group size supports the ‘many-eyes’ effect that could be expected with aggregation (Elgar 1989). However, elk have been reported elsewhere to show no decrease in vigilance with increasing group size (Laundre et al. 2001, Halofsky and Ripple 2008). This discrepancy may be explained by the fact that the present study was carried out in a controlled setting in a single habitat type. Studies of wild elk included natural settings where, rather than adjusting vigilance levels in response to risk, elk may have adjusted group size instead. In other species, vigilance levels have been shown to vary temporally based on a prey’s exposure to a predator (Powell 1974, Caraco et al. 1980, Sullivan 1984, Poysa 1987). While these latter studies focused on avian taxa, there is no reason to believe the same phenomenon could not be present in ungulates. It could also explain why the ‘many-eyes’ effect was documented on Egli’s farm: elk in this study were semi-domesticated, and no predation events have ever been recorded in the eleven years elk have been kept on the farm (Peter Egli, pers. comm.). As such, predation risk in this study varied exclusively with factors related only to group size, i.e.: the likelihood of detecting an attacker (number of individuals scanning), and the likelihood of escaping given an attack (dilution effect).

That a significant effect of group size on vigilance was detected in the direction expected from the ‘many-eyes’ effect suggests that despite an existence relatively free from predation risk, elk in this study may still have perceived greater risk in smaller groups. However, decreased vigilance with group size can result from intra-specific foraging competition, which intensifies as group size increases (Krause and Ruxton 2002:46-47). In a study of two species of gregarious antelope, blesbok *(Damaliscus pygargus phillipsi)* and impala *(Aepyceros melampus),* Dalerum et al. (2008) concluded that decreased scanning with increased group size was a result of foraging competition. The authors also noted, however, that relationship between group size, vigilance and foraging may be highly variable between species. In the present study, competition could have caused individuals to consume as much food in as little time as possible. Although scanning and feeding in elk are not completely exclusive activities (Fortin et al. 2004), feeding does interfere with scanning. Therefore, elk would have scanned less as group size increased. If competition affected vigilance, it is difficult to determine to what degree. Roberts (2003) reported that the group-size effect has been observed in several studies of non-feeding animals, and suggested that decreased vigilance with group size cannot result solely from foraging competition. It is therefore unlikely that forage competition resulted in the entire effect observed here.

That scanning decreased with group size might also suggest that the rate was neither related to klepto-paracitism (monitoring conspecifics for clues about resource location and exploiting those resources once they have been detected) or conspecific aggression, as such behaviours should have increased scanning rate with increasing group size (Krause and Ruxton 2002:46-47). Scanning rate did increase as food density decreased, suggesting that a certain amount of conspecific monitoring to detect more profitable food patches did occur. This result was consistent across group sizes and was likely associated with missed-opportunity costs. It was inconsistent with the failure to find significant missed-opportunity costs in the GUDs study, and suggests that the hay that was always available to the elk was not regarded as a valuable foraging opportunity by the elk. Future work using GUDs and vigilance measures to evaluate group foraging behaviour should focus on disentangling the contributions of predation risk and competition in determining group-size effects.

Although ungulates have been shown to respond to visual, olfactory and auditory stimuli (Walther 1969, Lent 1974, Garner and Morrison 1980, Berger et al. 2001), we did not use olfactory or auditory cues to elicit fear responses in the elk. Olfactory cues, for example wolf urine, differ from auditory and visual cues in that they persist in the environment long after the cue has been emitted (Eisenberg and Kleiman 1972). Scent contamination of the small number of paddocks available for this research could have added greater variation to results of vigilance and GUD trials and delayed other components of the study. Such delays would have been undesirable given the short period of time available to conduct this research. Furthermore, aggression and site abandonment in response to olfactory fear cues have been shown to be extremely muted in predator-naïve *versus* predator-experienced moose (*Alces alces,* Berger et al. 2001). Again, due to the limitations in time to conduct experiments, responses to olfactory fear cues might not have provided the best indications of perceived risk. Muted responses to auditory cues, such as wolf and coyote calls, have also been observed in wild, predator-naïve ungulates (Berger et al. 2001). Conversely, Hodgetts et al. (1998) observed marked aggressive behaviour during, and elevated levels of alertness after exposure to an auditory stimulus in domesticated red deer (*Cervus elaphus*). Wild elk have been shown to increase levels of scanning during periods of wolf presence, suggesting a response to one or several of the cues mentioned above (Creel et al. 2008). Although both olfactory and auditory senses and responses to such cues are certainly important in the suite of anti-predator defenses of ungulates, due to logistic and time constraints, they were not considered here. Further research should investigate the effects of both acute and chronic exposure to olfactory and auditory predator cues on GUDs and vigilance.

Results from this study suggest that GUD might help us understand how managing predation risk using group formation could contribute to improved foraging opportunities and decreased predation risk that in the long term will contribute to individual fitness. Managing predation risk using group formation could be especially important where herbivores behave as time minimizers. This would allow foragers to spend less time exploiting resource patches and more time in a safe habitat. Results also suggest that the absence of opportunity for group formation could have conservation implications by impacting individual survival, in turn leading to population level effects.

This study suggests that GUD methodology is suitable as a means of measuring foraging behaviour across a range of group sizes, and is sensitive enough to detect differences in that behaviour in elk groups that varied in size by as little as a single individual. While encouraging, these results are from trials carried out under relatively controlled conditions, compared with the type of studies that might be possible with free-ranging animals. Applying a more direct increase in predation risk than only variation in group size, for example, reducing the visibility in feeding areas by erecting screens or barriers, or conducting studies in wild settings could allow a better test of a 'group size' effect on perceived risk and should be considered for later study. In general, further experimentation and refinement of the methodology is recommended, in both domestic and free-range systems, using the techniques and findings presented here.

General conclusion

The GUD methodology proved sensitive enough to detect differences in foraging behaviour in groups varying by just one individual. Elk had lower GUDs in feeding trials with larger groups. Neither dominant foraging behaviour, nor the interaction between group size and dominant foraging behaviour had a significant effect on GUDs. GUDs varied significantly with the presence of calves at the two group sizes tested. Groups with calves had lower GUDs than groups comprising only adults. Calf presence had no significant effect on scanning rate. Food density affected the scanning rate similarly for all group sizes, such that individuals scanned more at the end of a foraging bout when food density was low. The relative spatial position within a group while feeding did not affect scanning rate. Elk displayed a 'many eyes' effect by significantly decreasing scanning rate with increased group size. Results were unclear as to whether predation risk, increased foraging competition, or both, drove this response. This study, particularly the GUD component, supports the prediction that elk perceive greater risk in smaller groups. Further experimentation and development of this methodology should occur such that it may be used to assess foraging behaviour and decisions in groups of free-ranging ungulates.

While the model used to describe the demographics of introduced elk herds in Ontario was simplistic, considering only variation in survival for different group sizes, experimentation with GUDs supports the underlying principle of the model: that aggregated elk may be more adept at handling predation risk. As elk in the LOW re-introduction area continue to gain experience with predators, better development of anti-predator behaviours should be expected, and could contribute to further population increases.

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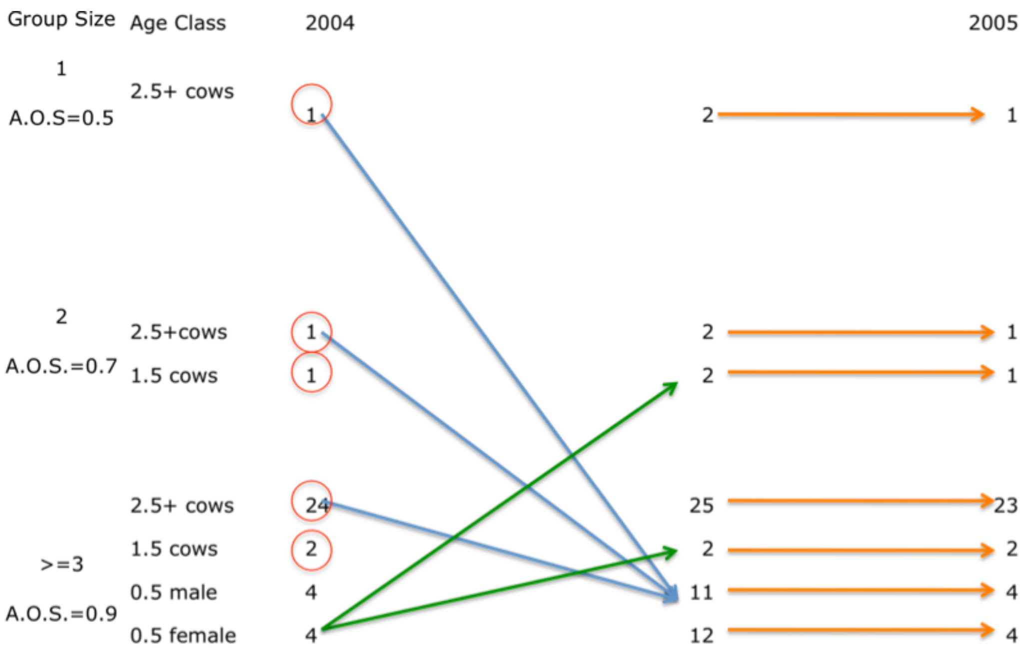
Appendix 1



- Red rings indicate 1.5 and 2.5+ year class animals that survived to spring 2004 and are assigned to the 2.5+ year class
- A number of the females assigned to the 2.5+ year class equaling the number of calves (0.5 year class) produced are assigned to group size 3+
- The number of remaining females assigned to the 2.5+ year class is divided by three and a third of this number is assigned to each group size category
- Blue arrows indicate females that contributed to calf recruitment
- Green arrows indicate calves to have survived winter that are then assigned to 1.5 year class
- Orange arrows indicate how and when survival probabilities are applied
- Survival probability for calves was 0.33
- Survival probability for 1.5 and 2.5+ year class animals in group size 3+ was 0.9
- Survival probability for 1.5 and 2.5+ year class animals in group size 2 was 0.7
- Survival probability for 2.5+ year class animals in group size 1 was 0.5
- Calves were only assigned to group size 3+
- Only 2.5+ year class females were assigned to group size 1