



## Foraging–vigilance trade-offs in a partially migratory population: comparing migrants and residents on a sympatric range

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Prey often suffer foraging costs associated with antipredator behaviours such as vigilance. Migration is one behaviour in ungulates that can lead to trade-offs between forage acquisition and predator avoidance. However, when forage intake is limited by food-handling time rather than by food encounter rate, ungulates can reduce foraging costs by synchronizing vigilance with chewing (multitasking). In this study, we compared patterns of vigilance, frequency of multitasking and total foraging time between migrant and resident individuals in a partially migratory elk, *Cervus canadensis*, population while they were together on their sympatric winter range. We used these comparisons to determine whether one herd segment had an advantage over the other in terms of forage intake and predator avoidance. Using observations of focal individuals, we found that residents were better than migrants at adjusting vigilance levels to spatial variation in wolf, *Canis lupus*, predation risk associated with a human-caused predation refuge. Migrant elk were less vigilant than residents where wolf predation risk was highest. Residents probably had an advantage over migrants because they were better at mitigating the foraging costs of vigilance by synchronizing vigilance with chewing. Migrant elk did not compensate for higher foraging costs by altering total activity time. Our study shows how foraging behaviours of free-ranging ungulates might contribute to demographic differences that lead to the loss of migratory behaviours.

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Migration is a common behaviour in ungulates that can lead to trade-offs between forage acquisition and predator avoidance (Bergerud et al. 1984; Fryxell et al. 1988; Hebblewhite & Merrill 2008). Populations can be partially migratory where some individuals remain on a single range year-round (residents), while others spend only a portion of the year on the sympatric range with residents and migrate to alternative ranges at other times of year (migrants). Several studies have examined the benefits of migrating by contrasting the amount of predation risk and forage resources that migrant and resident individuals from partially migratory populations are exposed to when on different ranges (Fryxell et al. 1988; Albon & Langvatn 1992; Kaitala et al. 1993; Ball et al. 2001; Hebblewhite et al. 2008; Hebblewhite & Merrill 2009). However, differences in experiences gained while occupying separate ranges may influence the foraging–predator avoidance trade-offs made while both groups are reunited on their sympatric range.

The need for ungulates to trade off foraging for predator avoidance can have important ecological consequences by indirectly

freeing plant communities from herbivory: a behaviourally mediated trophic cascade (Schmitz et al. 2004). For example, Christianson & Creel (2010) showed that forage intake rates of elk, *Cervus canadensis*, exposed to wolves, *Canis lupus*, were lower than those of elk that experienced no wolf predation. Other studies have shown that elk alter their foraging patterns in response to spatially heterogeneous wolf predation risk, so that plant communities in risky areas receive less herbivory than those in predation refuges (Grude et al. 2006; Ripple & Beschta 2007). However, a more recent study provided strong evidence against a behaviourally mediated trophic cascade in an elk–wolf system (Kauffman et al. 2010). Differences in experience with predators across study populations of elk could explain the inconsistent support for behaviourally mediated trophic cascades in the literature.

Two general hypotheses have been proposed to explain how differences in experience affect an animal's reaction to elevated predation risk. Traditionally, behavioural ecologists hypothesized that prey exposed to consistently high predation risk would spend more time scanning for predators (i.e. being vigilant) than prey that experience low risk simply because vigilant individuals are more likely to detect predators (e.g. Lima & Bednekoff 1999a). For example, moose, *Alces alces*, and elk with previous exposure to predators spent significantly more time vigilant when exposed to auditory and

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olfactory signals of predators than less experienced prey (Berger et al. 2001; Berger 2008). However, this view does not address how prey might alter vigilance temporally to maximize forage intake under the constraints of predation (Underwood 1982; Lima 1987).

The risk allocation hypothesis (RAH) accounts for the foraging costs of vigilance and proposes that the amount of vigilance expressed by an animal is a result of the temporal variation in its exposure to predation risk (Lima & Bednekoff 1999b). The RAH predicts that animals exposed to infrequent bouts of high risk are more likely to accept the foraging costs of increased vigilance while risk is high because they can make up for lost foraging time by increasing their foraging activity (and decreasing vigilance) during lengthy bouts of low risk. In contrast, animals exposed to more consistent levels of high risk must forgo vigilance and forage while risk is high to meet nutritional requirements. In a recent review, Ferrari et al. (2009) found mixed support for the RAH and attributed this to studies not meeting key assumptions of the hypothesis: that prey have perfect knowledge of the intensity and predictability of the risk regime, and forage requirements are a clear limiting factor for prey.

Another key assumption implicit in the RAH that was not recognized by Ferrari et al. (2009) is that foraging and vigilance are mutually exclusive (i.e. vigilance has a foraging cost), but this assumption is not necessarily true for herbivores in all situations (Illius & FitzGibbon 1994; Cowlshaw et al. 2003; Fortin et al. 2004a, b). For example, ungulates must stop harvesting bites while scanning for predators, but they can continue processing vegetation (i.e. chew) while being vigilant. Therefore, the amount of foraging costs due to vigilance will depend on whether forage intake is encounter- or handling-limited (sensu Spalinger & Hobbs 1992). During encounter-limited foraging, any time spent vigilant by an ungulate would reduce the amount of time spent searching for vegetation, reducing encounter rate, and therefore forage intake rate. During handling-limited foraging, however, ungulates encounter their next bite of vegetation faster than the current bite can be processed in the mouth, so they have 'spare time', which can be used to scan for predators without reducing forage intake (Illius & FitzGibbon 1994; Fortin et al. 2004a, b). As long as ungulates are handling-limited and synchronize vigilance with spare time, which is referred to as multitasking (Fortin et al. 2004a), vigilance should not have a foraging cost. Thus, the ability of ungulates to multitask may provide an additional explanation for the mixed support of the RAH in the literature (Ferrari et al. 2009).

Although studies have demonstrated that experience affects how prey respond to predators, we know of none that have considered the ability to maximize predator avoidance and forage intake simultaneously with the use of spare time. In this study, we compared how elk with different migratory strategies within a partially migratory population responded to changes in predation risk when foraging together on their sympatric winter range, where migrants and residents are not spatially segregated (Robinson et al. 2010). During our study, approximately 60% of the Ya Ha Tinda (YHT) elk population migrated 25–50 km west into the high elevations of Banff National Park (BNP), AB, Canada, in the summer (migrants) while the rest remained at YHT all year (residents). Hebblewhite & Merrill (2007) found that, once on their summer ranges, migrant elk were exposed to 15% lower wolf predation risk than residents, but for a short period (~5 days) during migration they were exposed to a 170% increase in predation risk. In contrast, resident elk were exposed to more consistent levels of risk than migrants during summer because of higher wolf densities at the YHT relative to summer ranges in BNP.

While resident elk were exposed to consistently high wolf predation risk during summer, they may have learned to maintain high levels of vigilance during periods of high risk without compromising forage intake by synchronizing vigilance with spare

time during handling-limited foraging. In contrast, because migrant elk experienced less predation risk from wolves during summer, they could have made up for lost foraging time during lengthy bouts of low risk and were not required to offset the foraging costs of vigilance by multitasking. If poor synchronization by migrants persisted during winter when both groups were exposed to similar wolf predation risk (Robinson et al. 2010), migrants would have been at a disadvantage, which could have contributed to the declining proportion of migrant elk observed in this population (Hebblewhite et al. 2006). We expected that, during winter, resident elk might synchronize vigilance bouts with spare time more frequently than migrants during handling-limited foraging, causing vigilance to be more costly for migrants (Fig. 1). To compensate for higher foraging costs of vigilance, migrant elk might spend less time being vigilant than residents, particularly when foraging outside the human-caused predation refuge at YHT (Fig. 1), where predation risk is highest (Robinson et al. 2010). Alternatively, migrant elk may have compensated for higher foraging costs of vigilance by spending more time being active, potentially foraging for longer throughout the day than residents (Fig. 1). To test these expectations we compared the amount of time spent vigilant, the spare time available (sensu Fortin et al. 2004b), the synchronization of vigilance with spare time and the total activity time between migrant and resident elk foraging on the YHT winter range.

## METHODS

### Study Site

The YHT is a 40 km<sup>2</sup> winter range located on the eastern slopes of the Rocky Mountains adjacent to BNP in Alberta, Canada. The YHT is used by Parks Canada to overwinter and train horses, so it receives a significant amount of human activity throughout the year (see Hebblewhite et al. 2006 for details). The majority of the YHT is native rough fescue (*Festuca campestris*) grassland interspersed with lodgepole pine (*Pinus contorta*) forests merging into Engelmann spruce (*Picea engelmannii*) at higher elevations, along with aspen (*Populus tremuloides*) forests and willow-bog birch (*Salix* spp.–*Betula glandulosa*) shrublands. Snow pack is generally less than 25 cm and patchily distributed due to consistent warm westerly winds throughout the winter (Morgantini & Hudson 1988), which, in combination with the high nutritional content of cured rough fescue (Pigden 1953), makes the YHT an ideal winter range for grazing ungulates. Elk are the dominant herbivore in the system; the population consisted of approximately 500 individuals during this study. Wolves, cougars, *Felis concolor*, and coyotes, *Canis latrans*, are the only active predators of elk during winter.

### Field Observations

Behavioural observations were made on 17 migrant and 19 resident VHF-collared (LMRT-4, Lotek Inc., New Market, ON, Canada) cow elk from 10 January to 25 March 2008. Elk were captured during 2001–2007 using a corral trap baited with hay between January and March when migrants and residents were together on the YHT winter range. VHF collars weighed 555 g (ca. 2% of an adult female's body weight) and were equipped with canvas strips designed to decompose over time. All capture and tagging procedures were approved by the University of Alberta Animal Care Committee (Protocol No. 353112; see Hebblewhite et al. 2006 for details). Resident elk were those that spent the majority of summer at the YHT, so we defined the migration strategy of each individual based on the percentage of summer days (15 June to 31 August during 2004–2007) that they were present at the YHT (for details, see Supplementary Material: Defining Elk Migration Strategy). Elk

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