

Daily Temporal Dynamics of a Large Mammal Predator-Prey System

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## ABSTRACT

### DAILY TEMPORAL DYNAMICS OF A LARGE MAMMAL PREDATOR-PREY SYSTEM

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Predation is a strong determinant of predator and prey behaviour, but little is known about diel predator-prey dynamics. Here I use GPS telemetry to evaluate drivers of wolf (*Canis lupus*) and moose (*Alces alces*) daily activity patterns in northern Ontario and examine how these patterns drive diel predation patterns during winter. Wolves and moose reduced velocity in warm periods of summer days, but showed little response to winter temperature. Both species increased velocity near dawn and dusk and tracked the timing of these periods throughout the year. Velocity of both wolves and moose increased kill rates of moose via encounter rate and prey detectability respectively. Crepuscular light had a negative influence on kill rate, contrary to previous hypotheses. This work shows how variation in movement parameters can provide novel insight into determinants of predator and prey activity patterns and in turn how these behaviours influence diel variation in predation.

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## General Introduction

Dynamic predator-prey interactions are increasingly recognized as important drivers of animal behaviour, wherein predators aim to increase hunting success and prey simultaneously aim to decrease predation risk (Sih 1984, Laundré 2010). The ramifications of these opposing goals are increasingly understood in a spatial context, but our understanding of fine-scale temporal predator-prey dynamics remains limited. Several studies have attempted to examine predator-prey diel dynamics by analyzing associations between predator and prey activity levels through the day (e.g. Arias-Del Razo et al. 2011, Eriksen et al. 2011, Ross et al. 2013), wherein a positive association between predator and prey activity levels is assumed to indicate that predators are tracking periods of high prey availability, and a negative correlation indicates prey avoiding periods of risk. While these studies have yielded important insight into complexities of these systems, they typically fail to yield a mechanistic understanding of these patterns. Principally, they are limited by minimal investigation of predator and prey behavioural responses to environmental stimuli, compounded by limited understanding of the mechanistic drivers of diel variation in kill rates.

Investigations of simultaneous predator-prey activity patterns typically lack an understanding of how both predators and prey respond to diel variation in environmental stimuli. Correlation between predator and prey activity levels could simply be spurious results from similar behavioural responses to environmental conditions, rather than the result of direct predator-prey interactions. Similar thermoregulatory needs, for example, could produce synchrony in their activity patterns that appear to represent predators tracking periods of high prey availability, despite the correlation being driven by factors

independent from predation. Though it remains difficult to determine true causal drivers of these patterns, we may further our understanding of these temporal dynamics by investigating the behavioural responses of predators and prey to environmental conditions, particularly in the context of the influence of these conditions on kill rates.

While it is commonly assumed that periods of high predator and prey activity are periods associated with high kill rates (e.g. Ross et al. 2013), this hypothesis lacks empirical testing. Theory predicts positive associations between kill rates and the movement rates of predators and prey through increases in encounter rate and prey detectability (Hutchinson and Waser 2007, Avgar et al. 2011), but the applicability of these principles to temporal predation dynamics has yet to be examined. Furthering our understanding of the mechanistic drivers of kill rates through the diel cycle may increase our understanding of temporal interactions between predators and prey, and provide empirical support for the application of these principles in future work.

Herein I aim to examine the daily temporal dynamics of the wolf and moose predator-prey system in northern Ontario. In Chapter 1 I first investigate how wolves and moose adjust their diel patterns to environmental stimuli - namely temperature and light levels - over the course of the year. In Chapter 2 I then examine how diel variation in light levels and in predator and prey movement rates mechanistically drive diel variation in kill rates during the winter season. This work aims to further our understanding of the fine-scale temporal dynamics of predator-prey systems.



## **Chapter 1: The Influence of Ambient Light Conditions on Wolf and Moose Activity Patterns**

### *Abstract*

Daily activity patterns can potentially influence predation dynamics, but currently little is known about environmental constraints on predator and prey activity patterns. Here we demonstrate similar behavioural responses of wolves and moose to seasonal variation in environmental stimuli. Both wolves and moose increased velocity near dawn and dusk. This effect tracked large shifts in the timing of dawn and dusk through the year, contrary to the hypothesis that moose diel activity patterns are tightly constrained by rumination requirements. Both wolves and moose showed reduced movements during warm periods of summer days, but no behavioural response to temperature in winter.

**Keywords:** diel, wolf, *Canis lupus*, moose, *Alces alces*, activity patterns, crepuscular, rumination requirements,

## ***Introduction***

Daily activity patterns can have consequences for an animal's predation risk (Kronfeld-Schor and Dayan 2003) and foraging success (Rijnsdorp et al. 1981). These complex patterns are driven by a variety of influences, such as food availability (Brown and Kotler 2001, Kotler et al. 2002), digestive constraints (Cederlund 1989), and thermoregulatory needs (Theuerkauf 2009). Predator-prey dynamics are often hypothesized to influence the diel patterns of predators and prey (Fenn and MacDonald 1995, Griffin et al. 2005, Ross et al. 2013, Monterroso et al. 2013), whereby prey should avoid periods of elevated predation risk and predators should select for periods of exceptional hunting success (Sih 1984, Eriksen et al. 2011). Though these assumptions are frequently invoked to explain diel activity patterns (e.g. Theuerkauf 2009, Ross et al. 2013, Monterroso et al. 2013), supporting evidence is rare. Predators often concentrate their space use in habitats with high predation success (Sih 2005, Katz et al. 2013), but empirical evidence for predation risk influencing activity patterns is lacking.

One difficulty lies in determining whether predators and prey are truly responding to the behaviour of their counterpart, or if they are responding to stimuli wholly unrelated to predation (Eriksen et al. 2011). This is exacerbated by limited knowledge of the mechanistic drivers of predation through the diel cycle, an issue I aim to clarify in Chapter 2. Several studies have examined synchronicity between predator and prey activity patterns (Arias-Del Razo et al. 2011, Eriksen et al. 2011, Ross et al. 2013, Monterroso et al. 2013), but thus far lack an understanding of how predators and prey respond to diel variation in environmental stimuli. Correlations between predator and prey activity levels may simply be driven by similar responses to external stimuli, and

thus examining the influence of environmental conditions on predator and prey movement behaviour may further our understanding of temporal predator-prey dynamics.

Here I examine environmental influences on wolf and moose daily activity patterns. Ungulates commonly utilize diel patterns characterized by activity bouts for foraging at sunrise and sunset, and interspersed with short activity bouts throughout (e.g., Dulphy et al. 1979, Cederlund 1989b, Cederlund et al. 1989, Green and Bear 1990, Pépin et al. 2006, Lowe et al. 2010). While the cause of this timing remains unclear, it has been speculated that ungulates may be partially restricted to this general pattern by their rumination requirements (Cederlund 1989). Ungulate foraging is often limited by the passage rate of the rumen (Dulphy et al. 1979, Barboza and Hume 2006), and thus the timing of their foraging activity bouts at dawn and dusk may simply coincide with the schedule of rumen clearance. If such a restriction tightly constrains the timing of their activity bouts, ungulates may not be able to adjust the timing of their activity bouts to track changes in the timing of dawn and dusk, particularly at high latitudes.

Predators are believed to have higher hunting success when prey are mobile (Sih 1984, Hutchinson and Waser 2007, Avgar et al. 2011), so increased ungulate activity at dawn and dusk could provide predators with a useful means of enhancing predation success by investing hunting effort during periods of increased prey activity. This hypothesis predicts that wolf activity with respect to dawn and dusk should parallel that of moose, their primary prey.

There are also good reasons to expect that wolf and moose diel patterns may also be influenced by temperature. A recent meta-analysis of wolf diel patterns (Theuerkauf 2009) suggested that wolves are strongly influenced by thermal conditions, and wolf

activity levels have previously been linked to temperature (Harrington and Mech 1982). Moose are susceptible to thermal stress (Renecker and Hudson 1986a, Lenarz et al. 2009), and there is some evidence (albeit somewhat mixed) that temperature can influence moose diel behaviour. Moose exhibit a behavioural response to thermal stress under hot ambient conditions by shifting their space use towards areas of greater thermal cover (van Beest et al. 2012), but there is little evidence to suggest that they similarly adjust their diel activity patterns when temperatures exceed the thermal neutral zone (Lowe et al. 2010).

Here we test whether moose and wolf movement rates are highest at dawn and dusk throughout the annual cycle, and whether temperature influences these activity patterns as a co-variate.

### ***Methods***

We used GPS radio-telemetry data from wolves and moose to estimate the influence of light and environmental conditions on their respective velocities. All data were collected in several boreal forest study sites (Fig. 1) in northern Ontario, characterized by rolling topography, extensive water coverage, and a mosaic of conifer, deciduous, and mixed-wood forest stand types. Predominant tree species were black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). The study areas (Fig. 1) encompassed a range of forestry activity from a pristine to heavily managed landscape. Wolves are coursing predators of moose, and are typically believed to be continuously

hunting when moving (Mech and Boitani 2003). In our study sites wolves are the primary predators of moose, and moose are the primary prey of wolves, particularly during the winter months (Moffat 2012). Woodland caribou (*Rangifer tarandus*) were sparse, and white-tailed deer (*Odocoileus virginianus*) were not observed in the study areas. Beavers (*Castor canadensis*) were common and widespread.

Data on moose diel movement rate patterns were derived from 122 GPS collared individuals (49° N, -92° W, Fig. 1: site number 1) from November-March each year during 1995 – 2001 (Rodgers et al. 1996, Rodgers 2001). For the analysis of moose displacement rates, we used 60,062 moose 3D telemetry location fixes with a one-hour fix interval.

Wolf diel displacement patterns were examined using 57 GPS collared individuals from 37 wolf packs in three study areas: Pickle Lake (51.6° N, -90.9° W, site number 2 in Fig. 1), Auden (50.4° N, -87.5° W, site number 3 in Fig. 1), and Cochrane (49.9° N, -80.6° W, site number 4 in Fig. 1) (Anderson 2012, Moffatt 2012). We used 77, 491 wolf 3D telemetry locations with a 2.5-hour fix interval. We removed all location fixes < 1 km from a garbage dumpsite to remove the potential for human avoidance to influence our interpretation of normal behavioural patterns by moose and wolves (Theuerkauf 2009).

We obtained temperature data from the following Environment Canada weather stations: Atikokan, Sioux Lookout, Geraldton, Armstrong, Timmins, Kapuskasing, and Pickle Lake. Hourly temperature measurements were averaged among the stations nearest each study area. For each telemetry location fix we calculated the difference between the temperature at the time of the fix and the average temperature that day. We categorized the months of November to April as winter, and May through October as summer. We

recorded the time of sunrise and sunset from the U.S. Naval Observatory, and for each telemetry fix calculated the temporal proximity (i.e. number of minutes) between the midpoint of the fix interval and the nearest dawn or dusk event on that day. We similarly calculated the temporal proximity to the nearest yearly average dawn or dusk event.

We calculated diel activity patterns for wolves and moose over monthly intervals by splitting telemetry data by month and binning by interval midpoint into 16 time periods throughout the daily cycle. We calculated average movement speed (measured as displacement per hour between fixes) within these bins, as well as a suite of environmental variables for each species.

We used linear regression models to test the influence of season, light cycles, and relative temperature on movement speeds by moose and wolves. For each species, we first evaluated the effect of season, temporal proximity to a dawn or dusk event, temperature relative to the daily average, and an interaction between relative temperature and season on movement rates. To test whether moose velocity was influenced by seasonal shifts in the timing of sunrise and sunset we then used information-theoretic methods to compare a model incorporating time to average dawn or dusk within months and an alternative model assuming no change in dawn or dusk timing throughout the full year. We removed one moose data point outlier following visual analysis of model diagnostic plots. This data point corresponded to dawn in October, showing greatly exaggerated moose velocity possibly due to rutting behavior.

## **Results**

Moose exhibited predominately crepuscular activity patterns throughout the year, with velocity maxima shifting seasonally to coincide with the timing of dawn and dusk (Fig. 2). Velocity increased at sunrise and sunset ( $t_{186} = 4.67$ ,  $P < 0.001$ ), with an effect better predicted by the current timing of sunrise and sunset than by the yearly average ( $\Delta AIC = 1.64$ ). Moose had a lower overall velocity in winter than in summer ( $t_{186} = 8.65$ ,  $P < 0.001$ ), and the effect of relative temperature was significantly dependent on season ( $t_{186} = 3.12$ ,  $P < 0.01$ ), verifying the need for subsequent analysis within season. After analysis within season, moose moved significantly faster during cool periods of summer days ( $t_{92} = 2.08$ ,  $P < 0.05$ ), but were not significantly influenced by the relative temperature in winter ( $t_{93} = 1.34$ ,  $P > 0.05$ ). Multiple regression indicated that moose velocity was influenced by a combination of dawn and dusk proximity, season, and relative temperature ( $R^2 = 0.41$ ,  $F_{4,186} = 31.73$ ,  $P < 0.001$ ).

Wolf diel patterns varied considerably throughout the year, ranging from diurnal to crepuscular to nearly nocturnal (Fig. 2). Overall, however, wolves showed similar responses to environmental conditions as moose (full model  $R^2 = 0.47$ ,  $F_{4,187} = 42.24$ ,  $P < 0.001$ ). Wolf velocity increased at sunrise and sunset ( $t_{187} = 6.51$ ,  $P < 0.001$ ), clearly following seasonal changes in timing of sunrise and sunset ( $\Delta AIC > 10$ ). Wolves moved faster in summer than in winter ( $t_{187} = 7.20$ ,  $P < 0.001$ ) and the effect of relative temperature was dependent on season ( $t_{187} = 5.12$ ,  $P < 0.001$ ). Analysis within season revealed that wolves moved significantly faster during cool periods of summer days ( $t_{93} = 6.81$ ,  $P < 0.001$ ), but their velocity was not significantly influenced by relative temperature in winter ( $t_{93} = 1.12$ ,  $P > 0.05$ ).

## ***Discussion***

Wolves and moose exhibited remarkably similar responses to environmental conditions. Most notably, both wolves and moose increased movement rates near dawn and dusk and tracked seasonal changes in timing of crepuscular periods throughout the year.

This finding is inconsistent with the alternative hypothesis that moose diel patterns are tightly constrained throughout the year by rumination requirements. While their foraging bouts are driven by the schedule of rumen clearance, moose appear able to adjust the timing of these foraging bouts to seasonal shifts in the schedule of sunrise and sunset events. This suggests that moose adjust the schedule of rumen clearance to match the timing of sunrise and sunset. While we can only speculate about the underlying adaptive basis for these seasonal changes, one possibility is that moose are most mobile at dawn and dusk to utilize increased visual acuity in these conditions (Klassen and Rea 2008). This could lead to improvements in foraging rates and/or predator avoidance (Kunkel and Pletscher 2001, Cozzi et al. 2012). Further field data would be required to conclusively test these hypotheses.

While the reasons that moose are most active at dawn and dusk remains unclear, it seems quite likely that wolves take advantage of this opportunity to improve access to prey. Predators are commonly hypothesized to track temporal periods of prey availability (e.g. Theuerkauf et al. 2003, Eriksen et al. 2011, Ross et al. 2013, Monterroso et al. 2013), but empirical evidence for this phenomenon is weak. Several studies have examined the degree of overlap between predator and prey activity patterns (Arias-Del Razo et al. 2011, Eriksen et al. 2011, Ross et al. 2013), but it is rarely known if these



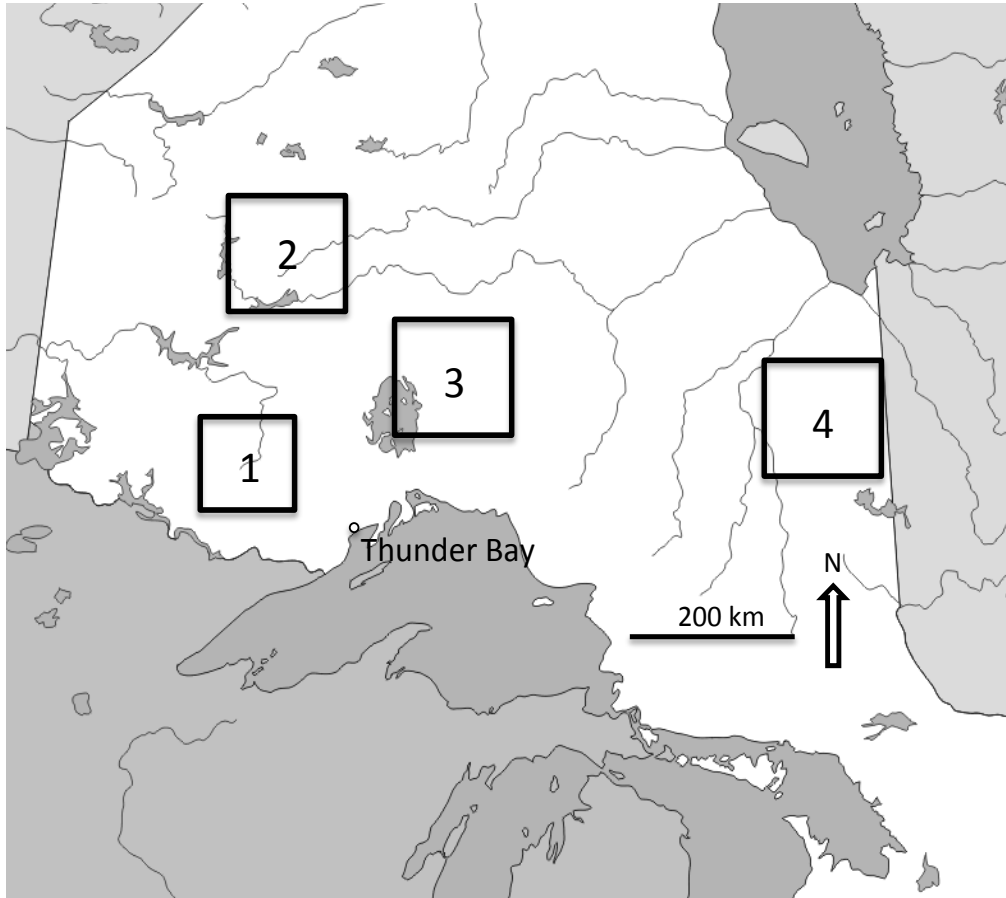
correlations are driven by predator-prey interactions or independent responses to environmental stimuli. At minimum, our results suggest that wolves track ambient light conditions associated with high moose movement rates.

Wolves and moose exhibited similar responses to temperature throughout the year. They both moved less during warm periods of summer days, but showed little response to temperature variation during the winter. In this respect our results differ from those of Lowe *et al.* (2010), who found no shift in moose diel patterns at temperatures above their thermoneutral zone. Given the influence of summer temperatures on moose demography (Lenarz *et al.* 2009), further examination of moose' behavioural responses to temperature is well warranted.

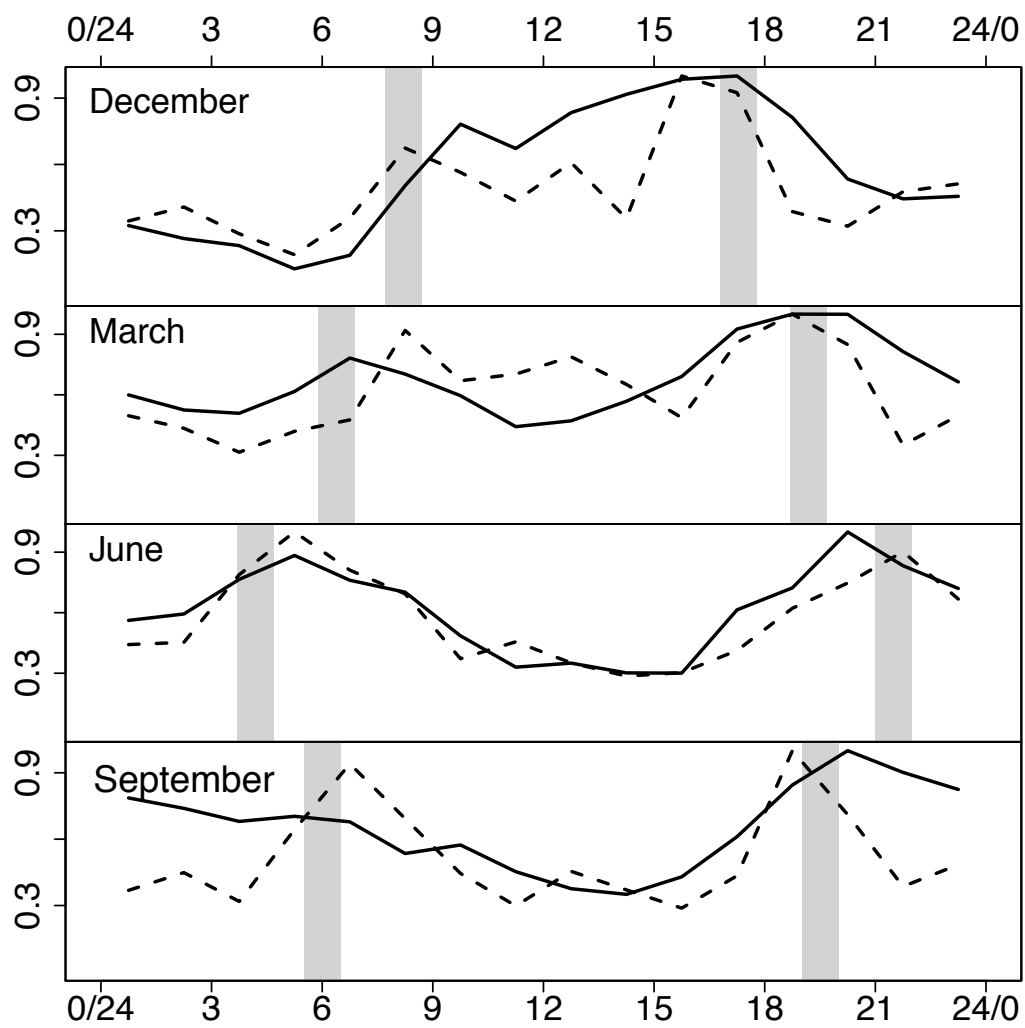
Seasonal variation in wolf and moose movement speeds is likely attributable to the physical impediment of deep snow during winter, and may be exacerbated by characteristics of each species. Snow provides a particular hindrance to young calves, and thus moose with calves would be expected to show substantially reduced movement rates (Telfer and Kelsall 1979). This effect may also have been exaggerated through changes in foraging behavior between seasons (Renecker and Hudson 1986b, Schwab and Pitt 1991). Wolf packs were typically largely sedentary for 60-120 hours at large prey carcasses in winter (unpublished data), but these long periods of sedentary behavior were largely absent in summer.

Data on wolf and moose diel movement patterns were collected in different years and different spatial locations. Our ability to make inferences on predator-prey interactions is therefore contingent on the generality of moose activity patterns. Similar diel patterns were shown by Lowe *et al.* (2010) suggesting consistency in their behaviour

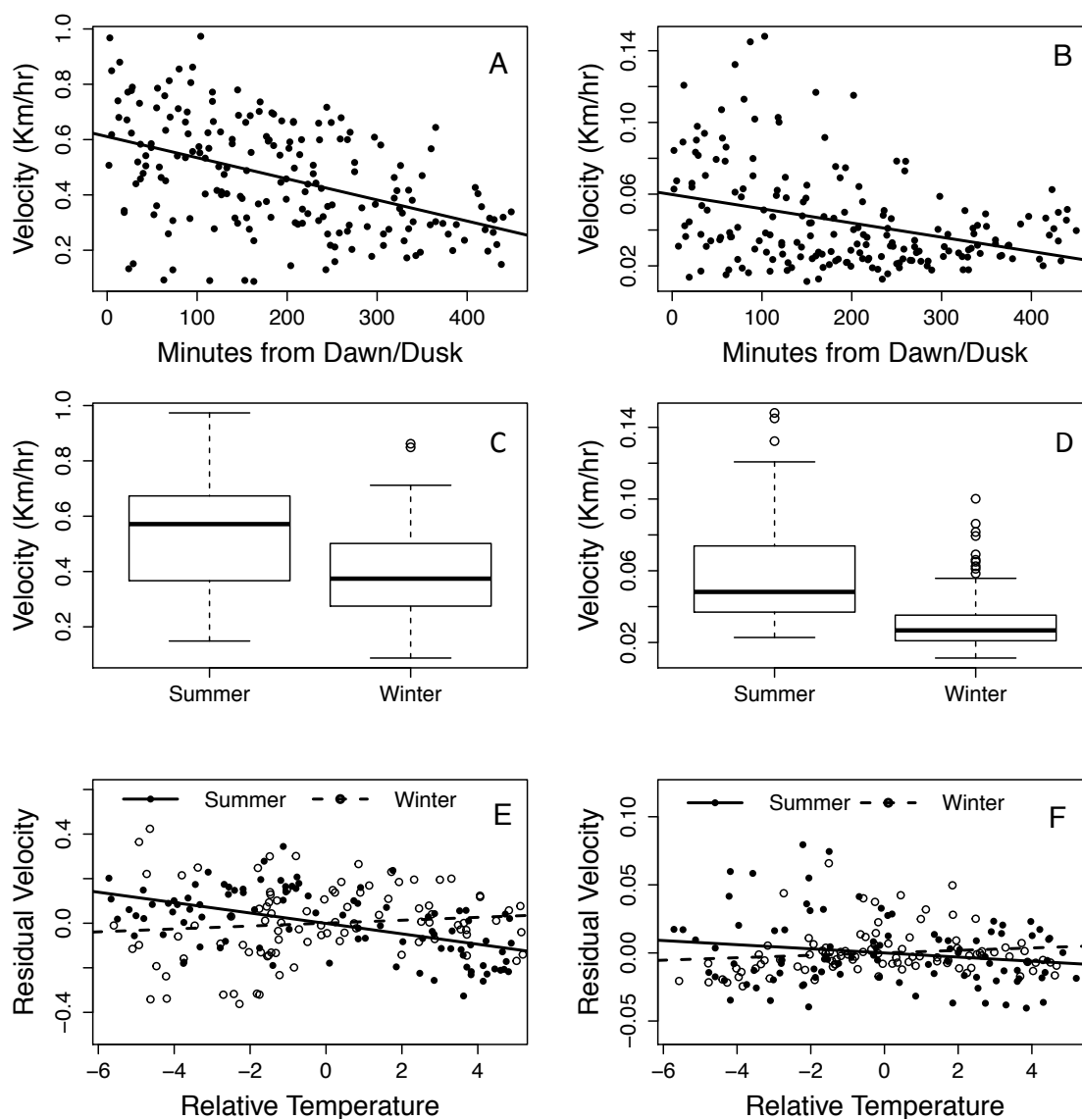
across similar landscapes, at least across Ontario. Similar behavioral patterns have also been seen in other ungulates in other places (Pépin et al. 2006). Hence, while further corroboration would certainly be helpful, we believe that our interpretations are useful as a working hypothesis at the very least.



**Figure 1:** Spatial locations of the moose study area (1) and three wolf study areas (2-4).



**Figure 2:** Wolf (solid) and moose (dashed) diel movement rate patterns through 4 months of the year. Grey areas represent dawn and dusk events. Note that wolf and moose movement rates have been normalized for visual clarity by dividing each velocity value by the month's maximum.



**Figure 3:** Influence of distance to dawn or dusk, season, and relative temperature on wolf (A, C, E) and moose (B, D, F) movement rates throughout the year. Data in panels E and F are residuals of panels A and B respectively, separated by season.

## **Chapter 2: Behavioral determinants of daily variation in wolf kill rates.**

### **Abstract**

Temporal variability in predation has important ramifications for ecological interactions, but surprisingly little study has been devoted to its causal factors. Diel variation in kill rate could stem from variation in encounter rate, prey detectability or both based on the logic underlying the ideal gas model. Here we use unique datasets on diel variation in kill rates and travel velocity of wolves and moose to predict daily temporal variation in kill rate. Our results suggest that the encounter rate between wolves and moose is the principle driver of kill rate. We also found evidence that prey movement rate has an additional influence on kill rate, exceeding that expected purely from its contribution to the encounter rate. We hypothesize that wolves more easily detect moose when moose are moving. However, this effect was countered by the negative influence of crepuscular light conditions on kill rate. We have shown that diel variation in predation primarily stems from variation in encounter rate and prey detectability, factors primarily driven by predator and prey movement speeds and crepuscular light conditions.

**Keywords:** kill rate, diel, wolf, moose, ideal gas model, temporal predation pattern, prey detectability, encounter rate

## Introduction

Variability in predation risk has important consequences for an animal's probability of survival (Preisser et al. 2005, 2007), space use (Brown et al. 1999, Sih et al. 2000, Sih 2005), and daily activity patterns (Fenn and MacDonald 1995, Sih et al. 2000, Railsback et al. 2005, Griffin et al. 2005). Recent work has begun to elucidate contributing causes of spatial variation in predation risk (e.g. Kauffman et al. 2007, DeCesare 2012, Courbin et al. 2013) yet we have minimal knowledge of the factors that influence temporal variability in these processes (Ferrari and Chivers 2009, Metz et al. 2012, Vucetich et al. 2012), particularly at fine scales. Specifically, although our understanding of sophisticated predator-prey behavioral interactions is increasing (Berger-Tal et al. 2010, Kotler et al. 2010, Courbin et al. 2013, Latombe et al. 2013), we lack a clear understanding of how predators and prey jointly influence diel variation in predation (Eriksen et al. 2011). This may be partially due to sizeable challenges in measuring fine-scale temporal variation in kill rate. Recent work has begun to focus on temporal dynamics of predation processes (e.g. Ferrari et al. 2008b, Metz et al. 2012, Vucetich et al. 2012, Latombe et al. 2013), but to our knowledge no study has fully examined the drivers of diel variability in predation risk in an any field setting.

One framework used to identify contributing causes of temporal variation in kill rate is the ideal gas model. This model, derived from the idealized linear movements of gas molecules, can be used to predict encounter rates between mobile objects, such as predators and prey, that move at a constant velocity in random directions (Hutchinson and Waser 2007). When applied to populations of predators and their prey, the ideal gas model predicts that the kill rate  $\phi$  should be proportional to the effective velocity of

predators and prey  $v$ , their densities  $N$ , and prey detectability  $\delta$  (Hutchinson and Waser 2007, Avgar et al. 2011):

$$\varphi \sim v\delta N,$$

where

$$v = \sqrt{v_{predator}^2 + v_{prey}^2}.$$

Here we define encounter rate as the rate at which prey occur within the predator's maximum detection range, and prey detectability as the probability of detection given an encounter. If animal density is assumed constant over the daily 24-hour cycle, then temporal variation in kill rate across the daily cycle must stem from variation in encounter rate, prey detectability, or both.

Here we use the logic underlying the ideal gas model to study the drivers of fine scale temporal dynamics between wolves (*Canis lupus*) and moose (*Alces alces*) in the boreal forest. Specifically, we test whether diel variation in wolf predation rates on moose vary with encounter rate and prey detectability. If diel variation in kill rate is primarily influenced by the encounter rate, then we predict kill rate to be positively related to the effective velocity of wolves and moose. Moose detectability may be influenced by variation in light conditions or variation in sensory cues available to wolves. In the first case, it has been suggested that wolves may have improved eyesight in crepuscular light relative to other times of day (Bekoff 1978, Theuerkauf 2009). In the second case, moose activity could itself influence sensory cues (i.e. scent, visual, and audible cues) used by wolves for prey detection (Sih 1984, Eriksen et al. 2011). The detectability hypothesis predicts that the rate at which wolves kill moose should be positively related to



crepuscular light availability, as well as moose movement velocity beyond its contribution to the encounter rate.

## **Methodology**

We used GPS telemetry data from wolves and moose to estimate kill rate and movement parameters. All data were collected in the boreal forest of northern Ontario, characterized by rolling topography, extensive water coverage, and a mosaic of conifer, deciduous, and mixed-wood forest stand types. Predominant tree species were black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). The study areas encompassed a range of forestry activity from pristine to heavily managed landscapes. Wolves are coursing predators of moose, and have been characterized as continuously hunting when moving (Mech and Boitani 2003). Wolves are the primary predators of moose in the boreal forest and moose are the primary prey of wolves, particularly during the winter months (Moffat 2012). Woodland caribou (*Rangifer tarandus*) were sparse, and white-tailed deer (*Odocoileus virginianus*) have not been observed in our study areas. Beavers (*Castor canadensis*) were common and widespread across all study sites.

Data on movement rates were derived from 122 GPS collared moose in northwestern Ontario (49° N, -92° W) in the winter period (November 7 to March 26) during 1997 - 2001. We used 26,032 moose 3D radio-telemetry location fixes with a one-hour fix interval to estimate moose velocity throughout the daily cycle.

Wolf hunting behavior was examined for 65 GPS collared individuals from 37

wolf packs in three study areas: Pickle Lake (51.6° N, -90.9° W), Auden (50.4° N, -87.5° W), and Cochrane (49.9° N, -80.6° W). We calculated wolf movement rates using 2.5-h fix intervals, and included data only from wolves that killed at least one prey, disregarding data < 150m from kills and < 1km from dump sites, yielding 23,558 relocations from 39 collared individuals. These selection criteria ensure that wolves were actually searching for new prey, rather than handling past kills or scavenging at a dump (McPhee et al. 2012, DeCesare 2012).

We calculated movement rates (km/h) for both predators and prey. We grouped predator and prey movement speeds into 16 intervals of 90-minute duration over the daily cycle, to ensure common time frame for subsequent comparisons. The movement speed between two consecutive locations (i.e. distance between successive locations divided by length of the fix interval) was assigned to the bin corresponding to the midpoint of the interval. Following the ideal gas model (Hutchinson and Waser 2007, Avgar et al. 2011) we used these data to calculate the effective velocity  $v$  of wolves and moose during each 90-min time interval.

We identified moose kills by investigating wolf telemetry location clusters (Webb et al. 2008) that occurred between November 7 and March 26 each year. All predation events were confirmed in the field as kills, rather than incidences of scavenging, based on signs of a struggle, separation of rumen content from the hair mat or carcass, and disarticulation of the joints (Webb et al. 2008). The time of each kill was assigned to the midpoint of the first location fix < 150 meters from the kill site, and was placed in the corresponding time interval. Although this assumption may have occasionally represented the time at which the wolves first confronted the moose without the

immediate death of the animal (e.g. Messier and Crête 1985), it effectively represents the time at which the wolves subdued their prey. We disregarded kills when a collared wolf was not within 150m of the kill site at the next location fix, or if the time of first arrival was ambiguous for other reasons. Ninety-four moose kills could be categorized with a temporal accuracy of 2.5 hours. Kills were then grouped by the same binning procedure as described previously for movement rate, yielding 16 estimates of kill rate (i.e. kills/90 mins) spread over the entire daily cycle.

We derived a crude metric of light conditions by producing a model of relative light availability through the diel cycle for each day of the study period. We assumed a one-hour twilight period with sunrise and sunset times taken from the U.S. Naval Observatory (Astronomical Applications Dept.). Crepuscular light availability  $\mu$  was calculated as the average proportion of a twilight period that occurred within each 90-minute bin. We calculated daylight availability  $L$  within each day of the study period, where  $L$  assumed values of one for daylight, zero for night, and 0.5 during twilight, and averaged each bin across the study period.

We tested kill rate temporal uniformity with a chi-square test, and used linear regression models to test the influence of the effective velocity and moose detectability on kill rate. We log transformed all variables to accommodate the multiplicative nature of the ideal gas model's predictors, after adding a value of one (1) to all measurements of light conditions and kill rate to allow log transformation. We tested the encounter rate hypothesis by modeling kill rate as a function of the effective velocity:

$$\varphi \sim v.$$

We tested the prey detectability hypothesis by adding the following variables to the ideal gas model: moose velocity, crepuscular light availability  $\mu$ , and daylight availability  $L$ , such that:

$$\varphi \sim v + v_{moose} + \mu + L.$$

and used a likelihood-ratio test to determine whether the inclusion of prey detectability significantly improved model performance. We used the statistical program R (Version 3.0, R Core Team 2013) for all analyses.

### ***Results***

Kill rate of wolves on moose was not constant through the day ( $\chi^2_{15} = 45.51$ ,  $P < 0.001$ , Fig. 2). The period of highest predation rate occurred in the early evening, (1630-1800) and was lowest in the early morning (0600-0730).

Effective velocity was a significant predictor of kill rate ( $F_{1,14} = 33.7$ ,  $P < 0.001$ ,  $R^2 = 0.71$ , Fig. 2A). Wolf velocity was approximately 13 times that of moose, hence effective velocity (which determines encounter rate) was almost purely driven by wolf movement (Fig. 1). On average, moose velocity contributed  $< 1\%$  to effective velocity. The rate at which wolves moved therefore dictated the encounter rate.

Kill rate was also related to factors influencing prey detectability. Moose velocity and crepuscular light availability were insignificant indicators of diel variation in kill rates when added to the ideal gas model independently. There was a substantial

improvement in fit, however, when both detection variables were added to the ideal gas model (likelihood ratio test  $\chi^2_2 = 15.22$ ,  $P < 0.001$ , full model  $F_{3,13} = 31.3$ ,  $P < 0.001$ ,  $R^2 = 0.89$ ). Kill rate showed a positive relationship with moose velocity ( $t = 3.92$ ,  $P < 0.01$ , Fig. 2B), but a negative relationship with crepuscular light conditions ( $t = -4.12$ ,  $P < 0.01$  Fig. 2C). The high correlation between these two variables ( $r = 0.67$ ) produces some uncertainty in the magnitude of the detection parameter estimates, but the likelihood profile demonstrates that the overall direction of these effects was nonetheless consistent across their 95% confidence intervals (Fig. 3). Kill rate was not influenced by daylight availability ( $t = -0.62$ ,  $P > 0.05$ ).

### ***Discussion***

Previous studies have suggested that diel variation in kill rate should be positively correlated with variation in predator velocity (Theuerkauf et al. 2003). Indeed, a predator's search rate (i.e. movement rate) is a central component of the functional response (Holling 1959), and can influence kill rates of mobile predators (McPhee et al. 2012b, but see DeCesare 2012). Here we go one step farther to demonstrate that the effective velocity of both predators and prey influences diel variation in kill rate through its influence on the encounter rate, as predicted by the ideal gas law. While this relationship has often been applied to predator-prey systems (Fenn and MacDonald 1995, Arias-Del Razo et al. 2011, Eriksen et al. 2011), direct empirical verification is surprisingly rare. We also provide evidence that prey mobility influences kill rate beyond the effect expected from its contribution to the encounter rate alone, although this effect is tempered by the negative influence of crepuscular light conditions on kill rate.

Changes in a predator's ability to detect its prey have been hypothesized to influence predation (Railsback et al. 2005, Griffin et al. 2005, Theuerkauf 2009, Kotler et al. 2010, Arias-Del Razo et al. 2011). It has also been suggested that variation in ambient light conditions can influence predation risk through its effects on prey detectability (Griffin et al. 2005, Getz 2009, Theuerkauf 2009, Kotler et al. 2010). Understanding the importance of each of these processes on predation, however, requires information on predator and prey movement rates, ambient light conditions, and the resultant kill rate. Here we show that moose movement rate contributed little to the encounter rate (Fig. 2), yet moose speed had a substantial subsidiary effect on kill rates. This suggests that moose movement speed had an impact on kill rate that was independent of its influence on the encounter rate. We hypothesize that this pattern may stem from the influence of prey mobility on the probability of detection.

There are several reasons to believe that the connection between prey mobility and detectability is important. The sensory cues that wolves use to detect moose are likely enhanced when moose are mobile. Wolves predominately use scent, vision, and auditory cues to detect moose (Mech 1966, Kunkel and Pletscher 2001). Prey activity levels influence transmission of all three types of sensory cues. Scent is more readily dispersed from an active animal than a sedentary animal (Peters and Mech 1975, Eriksen et al. 2011), and canids are better at visually detecting mobile objects than stationary ones (Miller and Murphy 1995), as is typical for predators (Sih 1984). Finally, moose can create a great deal of noise when they are moving (crunching snow, breaking branches, etc.), which would enhance auditory detection by wolves. Taken in sum, these processes would all act to increase the detection ability of wolves when moose are more mobile.

Our data suggest that wolves experience higher detection of mobile prey, but this effect was also influenced by lighting conditions. Crepuscular light conditions of dawn and dusk have been hypothesized to increase wolf hunting success (Theuerkauf et al. 2003, Theuerkauf 2009, Eriksen et al. 2011), but after controlling for variation in activity by both predators and prey, our results indicate if anything the opposite: a negative influence of crepuscular light conditions on wolf kill rate. This may be partially explained by a concurrent improvement in moose vision in crepuscular light (Klassen and Rea 2008), leading to improved ability of moose to avoid wolves, potentially negating any increase in wolf hunting success (Kunkel and Pletscher 2001). Dawn and dusk may then provide moose with opportunities for mobility in brief periods of lowered predation risk. This could partially drive moose crepuscular activity patterns, although we admit that this possibility remains speculative.

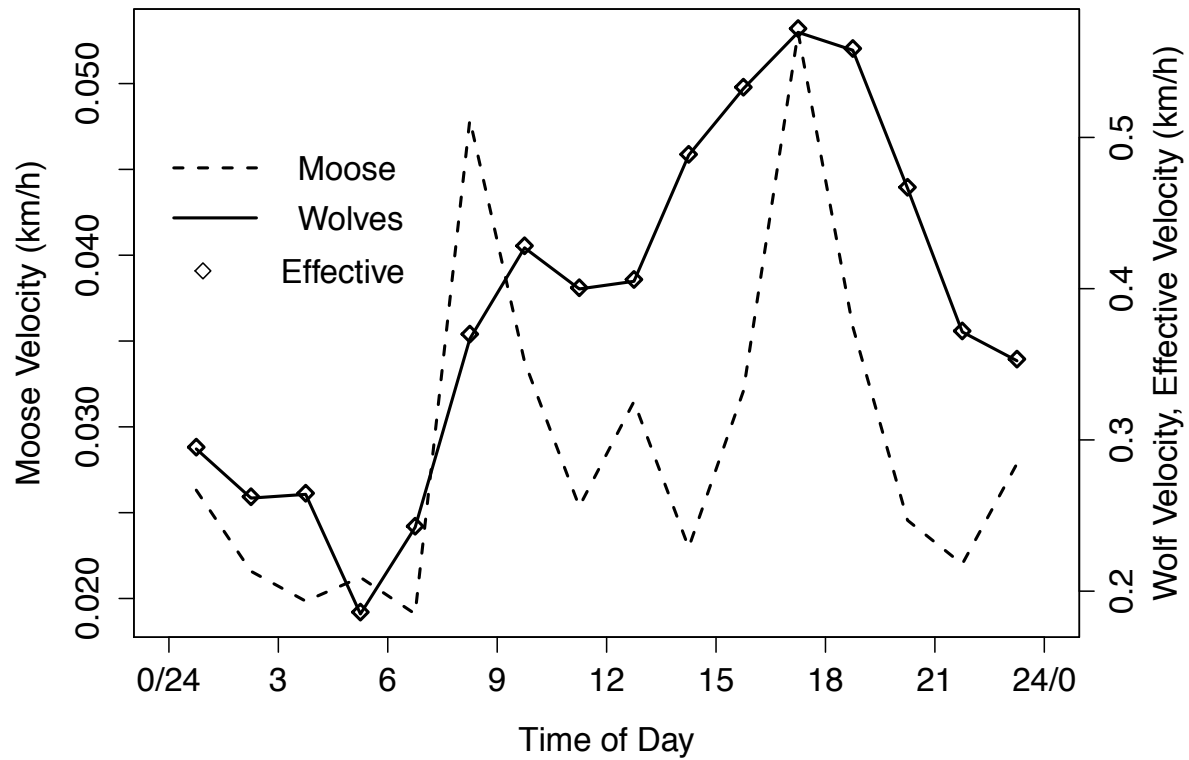
Diel activity patterns of predators and prey have been characterized as a behavioral response race (Lima and Dill 1990, Eriksen et al. 2011), wherein predators are speculated to allocate hunting effort to daily time periods of high efficiency, and prey attempt to avoid periods of high risk (Sih 1984). We have shown evidence for mechanistic links between predators and prey through their respective effects on predation. Our results suggest that the movement rates of predators and prey drive diel variability in predation through their respective influences on encounter rate and prey detectability. The diel movement patterns of predators and prey suggest a co-evolutionary arms race, via behavioral responses mediated by their obviously conflicting goals (Sih 1984).

Data on moose and wolves were collected from similar boreal systems, but at different times and locations. While this represents an obvious limitation, we nonetheless

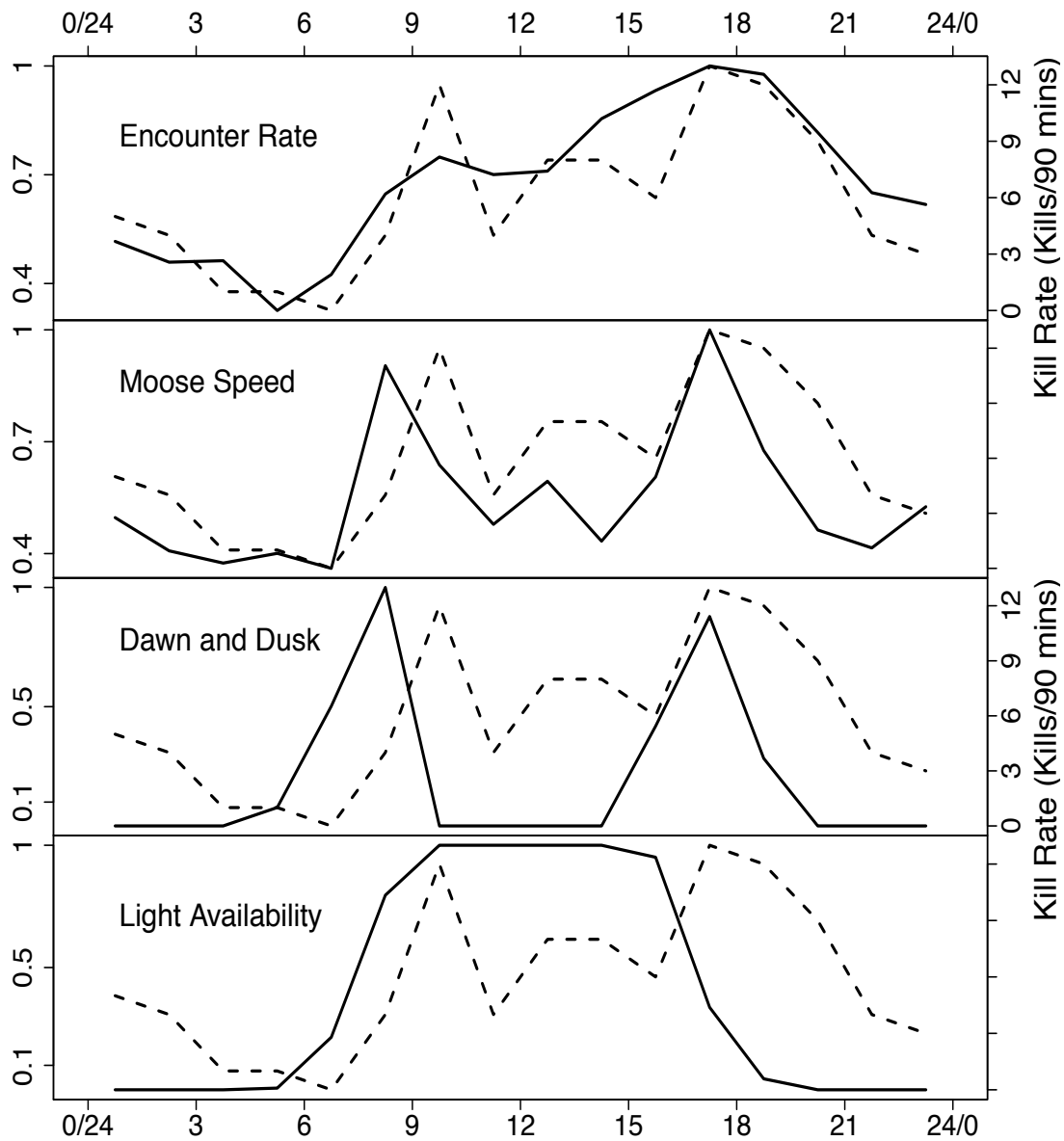
believe our interpretation is valid. The GPS radio-collared moose in this study were subject to predation by wolves, occurred in a landscape with similar habitat and climate characteristics as occurred in our wolf study areas, and had comparable densities of both moose and wolves. Hence, there is no obvious reason to expect differences in moose behavior across similar ecological landscapes. The validity of our assumptions is further corroborated by Lowe et al (2010), who demonstrated very similar patterns of diel movement rate for moose in central Ontario to those described here (see Lowe et al 2010, figure 7).

We have shown that diel variation in the rate of wolf predation on moose can be traced to two general mechanisms. The kill rate between predators and prey was positively related to their encounter rate, *sensu* the ideal gas model. We additionally provide evidence for the hypothesis that moose are more detectable when they are moving, but show that this effect is countered by the negative influence of crepuscular light on wolf hunting success.

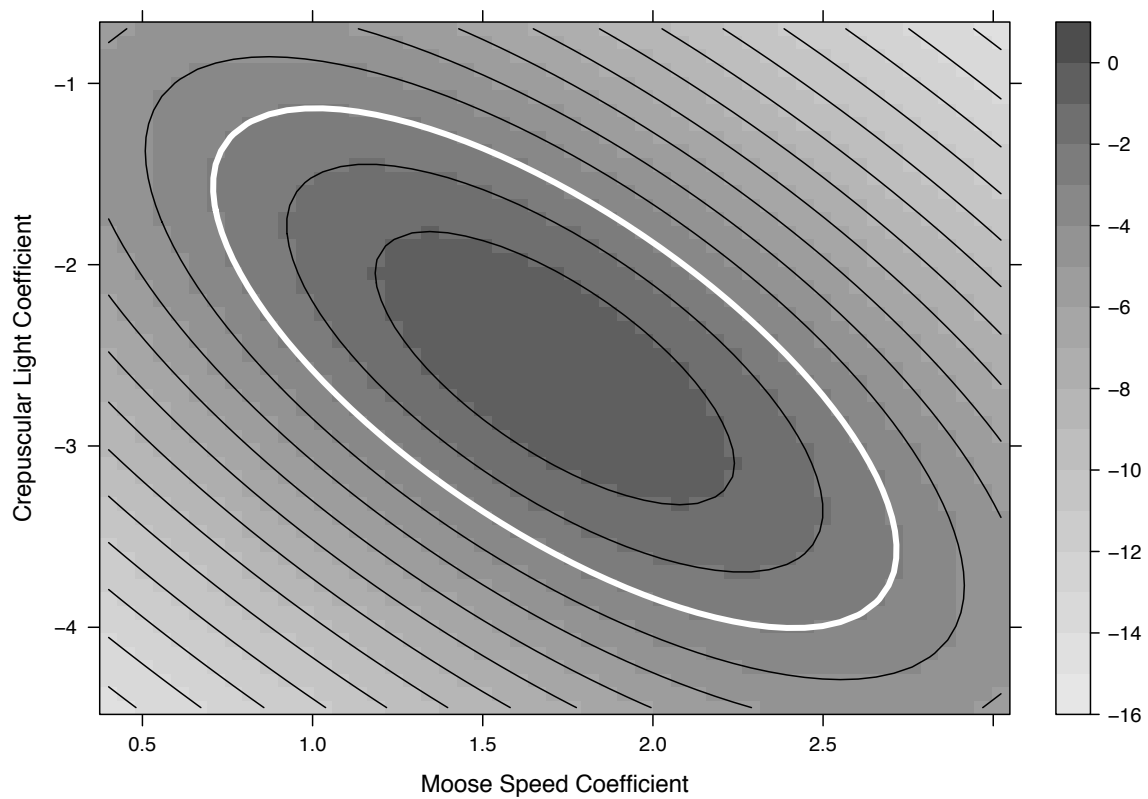




**Figure 1:** Daily movement rate patterns of wolves, moose, and their effective velocity in northern Ontario from November 7 to March 28.



**Figure 2:** Temporal pattern of kill rate (- -) plotted against effective velocity (A), moose velocity (B), crepuscular light availability (C), and relative light availability (D) through the 24-hour cycle. Kill rate was significantly related to the effective velocity, and the combination moose velocity and crepuscular light availability. Note that all predictor variables have been normalized by dividing by their maximum recorded value.



**Figure 3:** Likelihood surface for the influence of moose speed and crepuscular light availability on kill rates. White circle represents 95% confidence interval.

## Concluding Discussion

The principles of the ideal gas model have often been applied to describe temporal predator-prey dynamics, but empirical validation has thus far been lacking. Several studies have attempted to examine the diel behavioural response race between predators and prey by examining the synchrony of predator and prey activity patterns and drawing speculative inferences on how predators and prey may mold their diel pattern according to their counterpart (Arias-Del Razo et al. 2011, Eriksen et al. 2011, McCauley et al. 2012, Foster et al. 2013, Ross et al. 2013). The strength of these inferences may be increased with an understanding of how predators and prey behaviourally respond to diel variation in environmental stimuli. Predators and prey in our system showed very similar responses to environmental conditions. Of particular interest, both predators and prey increased velocity around dawn and dusk, and tracked the timing of these events throughout the course of the year. While their affinity for these crepuscular light conditions remains unclear, particularly for moose, the concurrent tracking of these events by both predators and prey hints at the potential influence of these periods on predation dynamics.

This work provides novel insight into the mechanistic drivers of diel variation in kill predation. The present finding that both predator and prey velocities positively influence kill rates via encounter rate and prey detectability supports the applicability of the ideal gas model to the temporal predation dynamics of predators and prey. Following the theory of predator-prey behavioural response races, mobile predators are speculated to allocate hunting effort to periods of prey activity, and prey may be expected to avoid exposure to periods of predator activity (Eriksen et al. 2011). These hypotheses are

frequently applied to the study of predator-prey dynamics, but this work represents the first empirical validation of their underlying mechanisms.

While predator and prey movement velocities yield simple predictions about predator and prey behaviour, these predictions must also be augmented by the influence of environmental conditions on kill rates. Wolves have previously been hypothesized to have greater hunting abilities during dawn and dusk through increased visual acuity (Theuerkauf et al. 2003), but our findings indicate if anything the opposite. This effect was partially obscured by the concurrent positive influence of increased moose movement rate on kill rates during these time periods, necessitating caution when elucidating diel predator-prey interactions. The negative influence of crepuscular light conditions on kill rates indicates that increased wolf velocity at dawn and dusk may be an attempt to invest hunting effort into periods of high encounter rate and moose velocity, rather than to take advantage of increased hunting abilities in these light conditions.

Behavioural response races between predators and prey are increasingly considered as important drivers of animal behaviour. While the impact of these interactions on their temporal interactions remains unclear, this work provides an important piece in furthering our understanding of the daily temporal dynamics in predator-prey systems.

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