

IMPLICATIONS OF CROPPING RATE VARIABILITY ON THE COSTS OF  
VIGILANCE

by

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A thesis submitted to the Graduate Council of  
Texas State University in partial fulfillment  
of the requirements for the degree of  
Master of Science  
with a Major in Wildlife Ecology  
May 2022

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## **ACKNOWLEDGEMENTS**

Funding for this study was provided by Texas State University, the Redwood National and State Parks, the California Department of Fish and Wildlife, as well as the Houston, Alamo, and Granite Bay Safari Club. Thank you to all the students who were involved in the field work: A. Duarte, J. Hunt, R. Keleher, L. Koetke, N. Kolbe, M. Longoria, R. Luna, M. O'Dell, L. Peterson, K. Richardson, S. Robinson, S. Shelton, G. Street, and D. Wolcott. Finally, I thank my parents Isabel and Victor as well as my siblings Reyne and Matthew for all of their love and support, from my move across the country to live in Texas through the completion of this Master's program.

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## ABSTRACT

Large grazing ungulates must forage for much of their active time to meet the energy demands of their massive bodies because they depend on nutrient-poor grasses and forbs. As such, maximizing efficiency of foraging bouts is selectively advantageous. Vigilance is a social and antipredator behavior that can result in reduced predation risk; however, vigilance directly competes with foraging and imposes an inherent foraging efficiency cost. As more time is allocated to vigilance, less time is available to forage. Using 199 focal observations of Roosevelt elk (*Cervus elaphus roosevelti*) collected in the Redwood National and State Parks of Northern California, I explored if increased elk cropping rate resulted in increased short-term forage intake and subsequently compensation for foraging time lost to vigilance. Notably, compensation via increased cropping rate is likely only feasible when food searching time is minimal and bite sizes are small, conditions that were satisfied in our study area. I developed and compared two novel models that describe possible mechanisms through which cropping rate compensation could occur. The Strategic Compensation Model illustrates a scenario where cropping rate compensation occurs due to an adaptative strategy by foraging elk to increase their cropping rate during periods of increased vigilance. In contrast, the Incidental Cropping Variability Model describes a situation where cropping rate variability is not strategic, but rather occurs due to the influences of social and environmental factors on cropping rate. I compared the proportion of time elk spent vigilant to their cropping rate (bites  $\cdot$  observation length<sup>-1</sup>). Four linear mixed-effect



model were estimated and compared using Bayesian Information Criterion model selection analysis. Three of the four models were identified as competing models, and each of the competing models contained the predictors: the proportion of the foraging bout spent vigilant, proportion of the foraging bout spent within one body length of a conspecific, time of day, and length of the focal observation. The influence of these predictors on cropping rate demonstrates that external factors influence cropping rate and supports the idea that cropping rate variability is incidental, occurs sporadically, and can compensate for vigilance in certain circumstances.

# **I. IMPLICATIONS OF CROPPING RATE VARIATION ON THE COSTS OF VIGILANCE**

## **Introduction**

Mammalian herbivores use 80-90% of their active time foraging to consume the large quantities of nutrient-poor, cellulose-rich food they need to satisfy their energy demands (Barboza et al., 2009). Life history traits including growth, survival, and reproduction depend on the use of energy obtained while foraging, thus foraging behaviors are directly linked to life history outcomes. As such, a propensity to maximize short-term forage intake rate is selectively advantageous (Parker et al., 1996). Short-term forage intake rate is dependent on a forager's mechanical constraints (i.e., cropping, chewing, encountering forage), the biomass and quality of local forage available for consumption, and decisions made by the forager including when, where, and how long to forage. Vigilance is an antipredator and social behavior that competes with foraging and is expressed by alertness and scanning behaviors that are used to detect predators and monitor the behaviors of conspecifics (Beauchamp, 2015; Bednekoff and Lima, 1998; Boggs, 1992; Quenette, 1990; Tatte et al., 2019; Treves, 2000). Increased efforts invested in vigilance can increase predator detection (Lima & Dill, 1990), decrease predation risk (Fitzgibbon, 1989), and avoid negative social interactions (Weckerly, 2001); however, increased vigilance can directly reduce time available to forage and possibly decrease food intake over a foraging bout (Houston et al., 1993; Djagoun et al., 2013; Robinson & Merrill, 2013). Currently, the magnitude of the impact of increased vigilance rates on herbivore foraging is unclear; thus, clarifying the relationship between foraging and vigilance is necessary to understand the consequences of vigilance behavior.

Predation is widely recognized as one of the strongest selective pressures on animals, and because of this, research investigating antipredator vigilance has dominated the literature in recent decades. Studies investigating the relationship between vigilance and foraging have identified factors that influence vigilance including predator presence (Meer et al., 2012), distance to cover (Dannock et al., 2019), body condition of prey (Winnie & Creel, 2007), group size of prey (Williams et al., 2003), and prey age and sex (Pecorella et al., 2019). Cropping rate is a component of short-term intake rate that is in part under an animal's conscious control, particularly when mechanical competition from chewing rate and bite encounter rate is low (i.e., bite sizes are small and palatable forage is ubiquitous during a foraging bout). Under these conditions, it is unknown if cropping rate is constant and dictated by an animal's size and morphology (Shipely & Spalinger, 1992), or if individuals fluctuate cropping rate under certain conditions. For example, perhaps when high rates of vigilance are needed in risky foraging scenarios, animals strategically increase their cropping rate to make up for foraging time lost to vigilance. A previous study examined this idea in elk, though empirical evidence in support was lacking (Kurpiers & Weckerly, In Press). Yet, it is possible that the previous study design lacked certain elements of realism by omitting potentially influential factors from the analysis such as time of day of the foraging bout and length of time the foraging elk spent in close proximity to a conspecific (Ager et al., 2003; Peterson & Weckerly, 2017; Peterson & Weckerly, 2018). Omission of these factors might have masked the occurrence of increased cropping rate as a vigilance mitigation strategy.

Illius and Fitzgibbon (1994) presented the possibility of a different vigilance mitigation strategy which they termed "spare capacity" or "spare time." They speculated

that herbivores might be capable of scanning their environment while simultaneously chewing forage when bite encounter rate was high, effectively maintaining their rate of food intake and reducing the costs of vigilance (Illius & Fitzgibbon, 1994; Fortin et al., 2004a). Overlapping the time needed to chew forage with a vigilant period could increase foraging efficiency; however, when animals detect threatening stimuli, they have been noted to stop chewing and focus entirely on the stimulus (Dannock et al., 2019) perhaps because chewing might interfere with predator detection (Blanchard & Fritz, 2007).

I investigated cropping rate variation as a behavioral modification that might mitigate the costs of increased levels of vigilance on short-term forage intake. Increased cropping rate can generate greater energy intake for elk compared to seeking bigger bites given certain cropping rates and bite sizes (Supplementary Figure 1, Weckerly, 2017), and cropping rate is a component of short-term intake rate that might be influenced by its own set of drivers. I pose the question: Under circumstances when cropping rate faces negligible interference from chewing rate and bite encounter rate, is cropping rate constant across varying levels of vigilance? If cropping rate is not constant, what factors might drive its variability? Exploring the form of the relationship between vigilance and cropping rate (a surrogate for food intake rate in an environment where bites are similar in size) will allow us to better define the effects of vigilance on cropping rate and short-term intake rate. To answer these questions, I propose two competing models that examine the relationship between cropping rate and the proportion of time during a foraging bout that an animal spends vigilant.

Because I wanted to investigate the relationship between cropping rate and vigilance when cropping rate was the main driver of short-term intake rate, our study was

conducted in a setting where instantaneous intake rate was predominantly influenced by cropping rate facilitated by minimized food searching time and small bite sizes due to the growth pattern, size, and age of forage (Illius & Fitzgibbon, 1994). Grassland habitats grazed by elk in the temperate meadows of Northern California in early winter meet both stipulations because the available grasses and forbs are young and short with tender tissue resulting in small bites that can be swallowed or quickly masticated, reducing competition between the processes of chewing and cropping (Greaves, 1978; Weckerly, 2017). The meadow habitat also carpets the environment with abundant palatable forage, minimizing food searching time (Greaves, 1978).

The Strategic Compensation Model (SC Model) postulates that, as the proportion of time spent vigilant while foraging increases, an animal increases its cropping rate (bites per unit time), causing increased short-term intake rate during the foraging period and compensating for some of the costs of increased vigilance (Fig. 1). As illustrated by the green shaded area in Figure 1, if cropping rate compensation is occurring, the slope of the function would have an absolute value less than the cropping rate when the head is down for the entire foraging period (intercept coefficient labeled  $CR_0$ ). Conversely, if cropping rate compensation does not occur, the slope of the function would have an absolute value greater than the cropping rate when the head is down for the entire foraging period (purple shaded area). If cropping rate is constant across a range of proportions of time the head is up, then the absolute value of the slope of the function will be similar to the cropping rate when the head is down for the entire foraging period (blue function).

The Incidental Cropping Rate Variation Model (ICV Model) illustrates a scenario where cropping rates are variable due to other factors apart from a strategic decision to compensate for vigilance costs (Fig 1). As previously described, chewing and food searching time must both be restricted for this model to detect that cropping rate variability is not driven by an adaptive animal behavior alone. Other factors included in this model are time of day when foraging, proportion of time forager spends within one body length of a conspecific, number of animals in a foraging group, and sex and age composition of animals foraging in a group (Thouless, 1990; Peterson & Weckerly, 2018). Ungulates such as elk are most active during dusk and dawn hours (Ager et al., 2003), and their digestion and energy use might be linked to their activity and rest regimens causing them to be hungrier and therefore more incentivized to forage at certain hours of the day thus influencing cropping rate. Foraging in close proximity to conspecifics also increases vigilance levels which can decrease cropping rate and, in turn, forage intake (Peterson & Weckerly, 2018). Lastly, group size and composition of group members likely also influences cropping rate as increased food competition can increase foraging intensity and speed (Thouless, 1990). To illustrate the possibility of external factors driving cropping rate variability, the ICV Model is a regression with a variable intercept but a constant slope (Fig. 2). The slope is constant because previous studies show that ungulates generally spend between 0 – 30% of foraging bouts in a vigilant state (Weckerly, 2017; Pecorella et al., 2019), and this narrow range might constrain slope variation. The cropping rates when HU is 0 illustrated by  $CR_H$  and  $CR_L$  in Figure 1 show two possible regressions with higher and lower y-intercepts caused by incidental factors

affecting cropping rate likely resulting in differences in overall food intake during a given foraging bout.

To evaluate the two competing models presented, I observed free-ranging Roosevelt elk as they foraged. I compared the predictions of the Strategic Compensation Model and the Incidental Cropping Rate Variation Model to examine if fluctuating herbivore cropping rates might suggest that the costs of vigilance are variable.

## Methods

*Study Area.*— All elk behavioral observations were conducted in the Prairie Creek drainage of Redwood National and State Parks, California (41°24'N, 124°02'W) during January of 2015 and 2016. The Prairie Creek drainage area is composed of the 70 ha Boyes meadow complex and the 51 ha Davison meadow complex that lie approximately 3 kms apart (Peterson & Weckerly, 2017). This northern, coastal region of California has cool summers that rarely exceed 25°C, rainy and mild winters with average temperatures of 3–5°C. Annual precipitation is greater than 150 cm most years, with the heaviest rains falling from fall to early spring (Starns et al., 2015). During the winter season, annual and perennial grass species dominate the meadow grasslands and make up more than 80% of the plant species present (Peterson & Weckerly, 2017). Predominant grass species include California oatgrass (*Danthonia californica*), redtop (*Agrostis gigantea*), soft chess (*Bromus hordeaceus*), and reed canary grass (*Phalaris arundinacea*) (Weckerly et al., 2001; Starns et al., 2015). The meadow complexes are surrounded by a forested landscape composed primarily of coastal redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and Western hemlock (*Tsuga heterophylla*). Elk predators in the region include black bears (*Ursus americanus*) and mountain lions (*Puma concolor*) (Bowyer, 1981), and neither recreational hunting nor culling occur within the parks (Weckerly, 2017). Elk in the Prairie Creek drainage are year-round residents and are habituated to the presence of humans, as park visitors regularly view these elk at distances of 10 to 500 m.

*Data Collection.*— Foraging and vigilance behaviors of grazing elk were evaluated via focal observations collected from 200 m or closer to the animal being observed. Each elk



was observed only one time during each day of sampling. As most elk were unmarked and indistinguishable from others, it is possible that some elk were observed again on subsequent study days. Focal observations were conducted on individual elk that were foraging using digital voice recorders to record observations that ranged from 4 to 11 minutes in length with 77% of observations falling between 9 and 10 minutes. A focal observation terminated when the focal elk was no longer visible for observation. The start and end times when the focal animal lifted its head above its shoulders—with its head up, an elk is neither feeding nor food searching—were recorded to calculate the proportion of time the elk was ostensibly vigilant. The number of bites taken during the focal observation was tallied, and cropping rate was calculated as the number of bites taken  $\cdot$  focal observation length<sup>-1</sup>. I also recorded the sex of the focal animal, foraging group size, group type, chewing rate (bites taken  $\cdot$  focal observation length<sup>-1</sup>), the proportion of the foraging bout the elk spent within one body length of a conspecific, length of the focal observation, date, time of day, forage biomass in the sector (see below), and location in the meadow where the focal animals foraged. Group types were males or females in mixed sex groups, and males in male-only groups (Weckerly et al., 2001; Weckerly, 2017).

Forage biomass available in the meadows was estimated in 570, 0.25-m<sup>2</sup> plots measured in 10 sectors in both the Davison and Boyes meadow complexes (Weckerly, 2017). Delineating sectors insured that all parts of meadow complexes were sampled. In each sector, 10 to 40, 0.25-m<sup>2</sup> plots were measured at 10 m intervals along randomly selected transects. Vegetation height and percent cover of palatable grasses, forbs, and shrubs was estimated using Daubenmire coverage classes (Daubenmire, 1968). In both

2015 and 2016, plant clippings to ground level in 129 randomly chosen plots were collected, sorted by type (grasses, forbs, or shrubs), dried, and then weighed to the nearest 0.1 gm. Multiple regressions using plant heights and coverage predicted dried biomass of grasses, and forbs and shrubs (Weckerly, 2017). These two regressions were then used to estimate biomass from average height and coverage measurements taken in each of the 570 plots.

*Analysis.*— I estimated four linear mixed-effects models to assess the effects of foraging in close proximity, duration of observations, available forage biomass, sex and age composition of foraging groups, and time of day on the response variable cropping rate in addition to the proportion of time spent vigilant (HU) which was a predictor in all four models. Group size was not included as a predictor in the analyses because group density is linked to increased social interactions that disrupt foraging behavior in Roosevelt elk, whereas group size is not related (Weckerly, 1999), and vigilance is influenced by group density but not group size (Peterson & Weckerly, 2018). This favored the inclusion of the predictor the proportion of time spent within one body length of a conspecific (Prop1BL) over group size, which have a low correlation with each other ( $r = 0.23$ ). Linear mixed effects models were estimated due to the possibility of repeated measures on individual elk; focal elk may have been observed on multiple days because most elk were untagged and indistinguishable from one another (Bates et al., 2015; Peterson & Weckerly, 2018). The simplest model estimated solely the effects of HU on cropping rate ( $\text{bites} \cdot \text{min}^{-1}$ ). This model contained the fundamental predictor being investigated—time spent vigilant—to assess whether vigilance levels alone explained the majority of the variation in cropping rate. The second model estimated the effects of the proportion of time

foraging within one body length of a conspecific, time of day, and duration of the observation. The third model estimated whether changes in sex and age composition of a foraging group, in addition to the predictors in the second model, coincided with cropping rate shifts. In the fourth model, I added biomass to the third model to gauge whether fluctuations in available biomass were influencing cropping rate. The random factor for each model was the day of focal observation coded to year and Julian date (e.g., January 5, 2009 was five09) with an intercepts random effect (Bates et al., 2015; Peterson & Weckerly, 2018). A Bayesian Information Criterion (BIC) was used to evaluate which of the models best fit the data. Additionally, for each model the marginal  $r^2$  was estimated to show the variation in cropping rate accounted for by the fixed effects, and the condition  $r^2$  was estimated to show the variation in cropping rate accounted for by both the fixed and random effects (Nakagawa & Schielzeth, 2013). Using a parametric bootstrap, I calculated the 95% confidence intervals of the fixed and random intercept estimates of each model. The model was bootstrapped 1,000 times and estimated using the lme4 package in program R version 4.0 (R Core Team, 2020).

## Results

Of the 199 focal observations collected of foraging elk, 143 were of female elk, eight were of males in mixed sex groups, and 48 were of males in male-only groups. The mean elk cropping rate was  $35 \text{ bites} \cdot \text{min}^{-1}$  (min:  $2 \text{ bites} \cdot \text{min}^{-1}$ , max:  $80 \text{ bites} \cdot \text{min}^{-1}$ ), and the mean HU was 0.14 (min: 0.00, max: 0.87) (Table 1). The average proportion of time a focal elk spent within one body length of another elk was 0.23 (min: 0, max: 0.90), average length of the focal observation was 9.17 min (min: 4 min, max: 11 min), average forage biomass was  $273.95 \text{ kg} \cdot \text{ha}^{-1}$  (min:  $148 \text{ kg} \cdot \text{ha}^{-1}$ , max:  $496 \text{ kg} \cdot \text{ha}^{-1}$ ), and the average time of day that the focal observations were collected was 12:17 pm (earliest: 6:00 am, latest: 5:10 pm) (Table 3). The model selection analysis identified that three of the four models were competing because their BIC values all fell within 2 units of each other (Table 2). In each of the three competing models, the predictors proportion of time with the head up, proportion of time spent within one body length of a conspecific, duration of the focal observation, and time of day all influenced the response variable cropping rate (Table 3). Thus, I selected the model with the fewest predictors which also had marginal and conditional  $r^2$  values that were similar to competing models. The selected model had a y-intercept of  $24.68 \text{ bites} \cdot \text{min}^{-1}$  with a parametrically bootstrapped 95% confidence interval of 14.87 to  $34.74 \text{ bites} \cdot \text{min}^{-1}$ . The slope was -49.90 indicating that the absolute value of the slope was greater than the y-intercept. The additional predictors were useful in accounting for at least some of the variability in cropping rate from 0 to 0.2 HU (Supplementary Figure 1).

## Discussion

Our study expands on the concept that cropping rate variability could compensate for elevated vigilance initiated in Kurpiers and Weckerly (In Press). Kurpiers and Weckerly (In Press) evaluated elk foraging data through the lens of the Strategic Compensation Model and found that Roosevelt elk had a constant cropping rate across a spectrum of vigilance levels; however, the results of this study contradict that finding. I found that the slope of the selected regression was greater in absolute value than the y-intercept, indicating that strategic compensation did not occur, nor was cropping rate a constant across vigilance levels (Figure 1). If cropping rate and vigilance were directly proportionate to each other, the absolute value of the slope and y-intercept of the regression would be equal such that when an elk spends 100% of a foraging bout vigilant, cropping rate is 0. Our regression had an absolute value of the slope greater than the y-intercept therefore showing that elk decrease cropping rate more rapidly as vigilance increases. Our study introduced a novel paradigm, the Incidental Cropping Rate Variability Model, to compare against the SC Model and discern whether vigilance compensation was feasible outside of the Strategic Compensation Model. The ICV model posits that cropping rate is variable and can reduce the costs of vigilance in certain instances, and periods of compensation are not deliberate, but rather induced by environmental and social factors. I found that elk cropping rate is influenced not only by the amount of time spent vigilant, but also by the proportion of time foraging that was spent within one body length of a conspecific, the time of day, and the duration of the focal observation. These findings support the ICV model and indicate that cropping rate

variability does occur and could feasibly increase forage intake rate through increased cropping rate under particular circumstances.

Certain conditions of the forage available in these grassy meadows were ideal for assessing whether compensation was occurring by cropping rate variability or not. For increased cropping rate to result in increased forage intake over a foraging bout, cropping must not be impeded by any other physical foraging processes; elk must be able to take bites quickly with minimal foraging time lost to searching for and chewing food. Weckerly (2017) demonstrated that during the winter in this study site, there was no correlation between cropping rate and chewing rate meaning that there was no competition between these two processes. This is because the low levels of available forage biomass resulted in relatively small bites sizes that likely ranged between 0.025 – 0.15 gm with little opportunity for bites greater than 0.5 gm (Fig. 3.1, Weckerly, 2017). Bites that are larger than 0.5 gm can cause competition between cropping and chewing and cause subsequent cropping rate decreases as time spent chewing bites dominates more foraging time (Wickstrom et al., 1984; Gross et al., 1993). Additionally, because this meadow habitat was densely carpeted by grasses and forbs, very little time was needed to search for forage, thus cropping rate was not hindered by excessive food searching (Bradbury et al., 1996). This young-growth grassland setting was ideal for distinguishing factors that influenced cropping rate, apart from chewing rate and food searching time whose influences on cropping rate are well-documented (Spalinger & Hobbs, 1992; Bradbury et al., 1996).

Cropping rate was influenced by the proportion of a foraging bout spent within one body length of a conspecific which aligns with literature on both ungulate foraging

competition and elk social dynamics (Thouless, 1990; Ceacero et al., 2012). Thouless (1990) showed that cropping rate of subordinate red deer (*Cervus elaphus*) decreased in proximity to dominant conspecifics while dominant individual cropping rates were unaffected, and Ceacero et al. (2012) found that higher social rank was positively correlated to the amount of time spent foraging during early stages of a foraging bout and to the energy content of forage. These studies show that social rank and dynamics undoubtedly influence foraging behaviors and food intake. In my study, the longer an elk spent in close proximity to a herd-member, the faster its cropping rate was which may imply that elk are incentivized to eat more quickly when they are facing competition for the choicest bites of forage (Peterson & Weckerly, 2018). Sex and herd composition did not influence cropping rate, but this result may be attributed to the inclusion of the predictor proportion of time within one body length of a conspecific. Elk have a social hierarchy in which male elk are dominant to females and juveniles, leading to social segregation by sex and subsequent differences in foraging behaviors and forage access (Weckerly et al., 2001; Bowyer, 2004). Furthermore, large, sexually dimorphic herbivores like elk ecologically segregate, meaning they differentially use habitat and food resources because larger males make different foraging decisions than females based on their greater metabolic requirements (Barboza & Bowyer, 2000; Mysterud, 2000), though there is evidence that this correlation can be weak in some instances (McGuire & Weckerly, 2020). Agonistic interactions between elk that cause foraging behavior adjustments require them to be in close proximity to each other, and thus the predictor proportion of time within one body length of a conspecific likely captured sex-related foraging influences on cropping rate. A linear mixed-effects model analyzing the

effects of the predictors HU, length of observation, time of day, and sex on the response variable cropping rate showed that sex did significantly influence cropping rate when the predictor proportion of time spent within one body length of a conspecific was excluded, supporting this idea (Kurpiers & Weckerly, In Press). This evidence gives insight into sex divergent elk foraging behavior; proximity should be considered as well as the sexes of interacting elk when investigating social segregation relating to foraging behaviors (Peterson & Weckerly, 2018).

The time of day of a foraging bout affected cropping rate. Previous work on elk activity patterns has shown that elk vigilance, the tortuosity of their foraging path, and the proportion of time they spend foraging are all influenced by time of day (Green & Bear, 1990; Peterson & Weckerly, 2018). Green and Bear (1990) found that elk use up to 85% of their time to forage during the hours surrounding dawn and dusk, contrasting with daytime hours when they would forage for at most 20% of their time. It is therefore unrealistic to separate elk habitat use and foraging behaviors from temporal variability, and time of day must be considered as a factor when describing foraging behaviors. Additionally, elk in Northern California have been noted showing relatively little activity during nighttime hours (Weckerly, 2017), which might further cause their daytime foraging patterns to vary as their hunger and therefore their motivation to forage fluctuates throughout the day.

Length of the focal observation also impacted cropping rate in that the longer the length of the foraging observation, the greater the cropping rate. This parameter is not germane to isolating and understanding the foraging behaviors I aimed to study, but it is useful in capturing a fine scale temporal effect that occurs when observations are short.



On short, green swards, there is motivation for elk to take fast bites to capitalize on time spent foraging, but this pattern may not be evident in shorter focal observations because periods of foraging when cropping rates are higher are interrupted by vigilance periods that preclude elk from taking bites. Elk forage in bouts that typically last 2 to 4 hours (Cook et al., 2016; Roberts et al., 2017), and ideally I would observe elk during hour- or day-long activity bouts to establish a more accurate estimate of their forage intake over a realistic time scale, though it would be difficult given the field conditions and restrictions present when working with wild elk populations. It would be valuable to focus future efforts on collecting longer foraging observations to better emulate real conditions of ungulate foraging. Though longer observations are preferred to capture accurate cropping rates, observations of shorter length (4 to 6 min) were deemed worthy of inclusion in analysis because the average cropping rate of  $35.4 \text{ bites} \cdot \text{min}^{-1}$  when all observations were included was similar to the average cropping rate when 4 to 6 min observations were excluded ( $36.5 \text{ bites} \cdot \text{min}^{-1}$ ). Furthermore, the average cropping rate of  $35.4 \text{ bites} \cdot \text{min}^{-1}$  ( $\text{SD} = 12.5 \text{ bites} \cdot \text{min}^{-1}$ ) is consistent with elk cropping rates reported in the literature (Gross et al., 1993; Fortin et al., 2004b; Peterson & Weckerly, 2018).

Available forage biomass is often linked to cropping rate due to its effect on bite size (Gross et al., 1993; Fortin et al., 2004b); however, this was not the case in our study despite the variability within the available forage biomass from  $148 \text{ to } 496 \text{ kg} \cdot \text{ha}^{-1}$  (Table 3). Yet, when compared to the  $100 \text{ to } 7000 \text{ kg} \cdot \text{ha}^{-1}$  range of forage biomasses typically encountered by elk in grassland environments (Fig. 3.2, Weckerly, 2017), the forage biomass present during this study was low. It is possible that biomass at the scale of the hectare was too broad and might not capture the true forage biomass variability at

the scale encountered by elk along their foraging path (Weckerly, 2017). To meaningfully measure forage biomass at the scale of the foraging path, a finer scale should be used, perhaps at the scale of the bite station (McGuire & Weckerly, 2020).

Cropping rate variability, rather than strategic cropping rate compensation, is likely the more realistic way to view the potential for cropping rate increases to result in compensation in response to vigilance in ungulates. In environmental settings where forage is relatively saturated and bite sizes are small, there may be instances when ungulates such as elk are able to increase their forage intake rate and offset some of the foraging time that is lost to vigilance. The multiple factors that influenced cropping rate identified in this study in addition to the amount of time elk spent vigilant indicate that compensation via increased compensation via increased cropping rate likely occurs incidentally and sporadically.

**Table 1.**— Summary of cropping rate (bites · min<sup>-1</sup>), proportion of time with head up, proportion of time spent within one body length of a conspecific, time of day, focal observation length (min), group size, and forage biomass (kg · ha<sup>-1</sup>) (n=199).

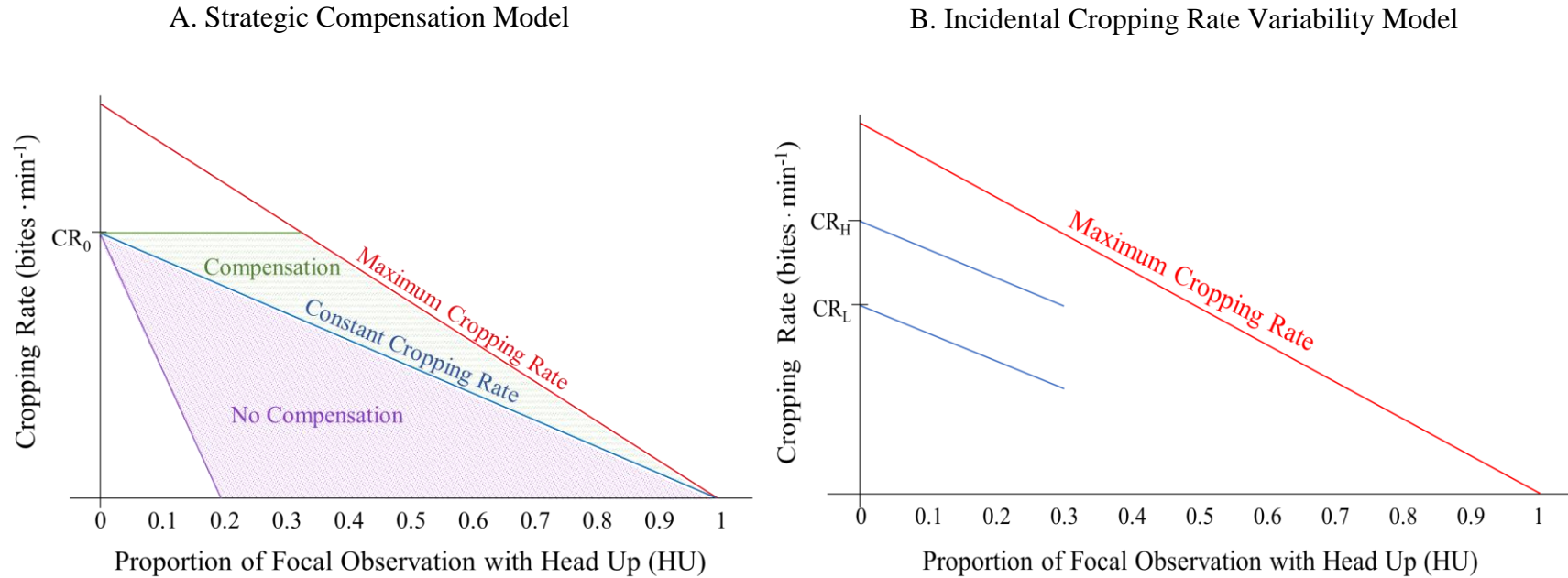
Variable	Minimum	First Quartile	Second Quartile	Third Quartile	Maximum	Mean	Standard deviation
Cropping Rate	2.20	26.35	36.50	43.20	70.90	35.39	12.48
Head up	0.00	0.03	0.09	0.19	0.87	0.14	0.16
One body length	0.00	0.00	0.14	0.37	0.90	0.22	0.25
Length of Observation	4.00	9.00	10.00	10.00	11.00	9.18	1.66
Time of day	6:04	9:30	12:17	14:33	17:10	12:17	2:47
Group size	3.00	47.00	47.00	50.00	50.00	37.53	18.81
Forage biomass	148.00	209.00	256.00	324.00	324.00	273.90	92.18

**Table 2.**—Summary of Bayesian Information Criterion model selection analysis of four compared models. Summary shows  $\Delta\text{BIC}$  values, number of parameters plus number of random effects estimated by each model, and marginal and conditional R-squared values. The random factor for each model was the day of the focal observation coded to year and Julian date. The selected model is denoted with bold font.

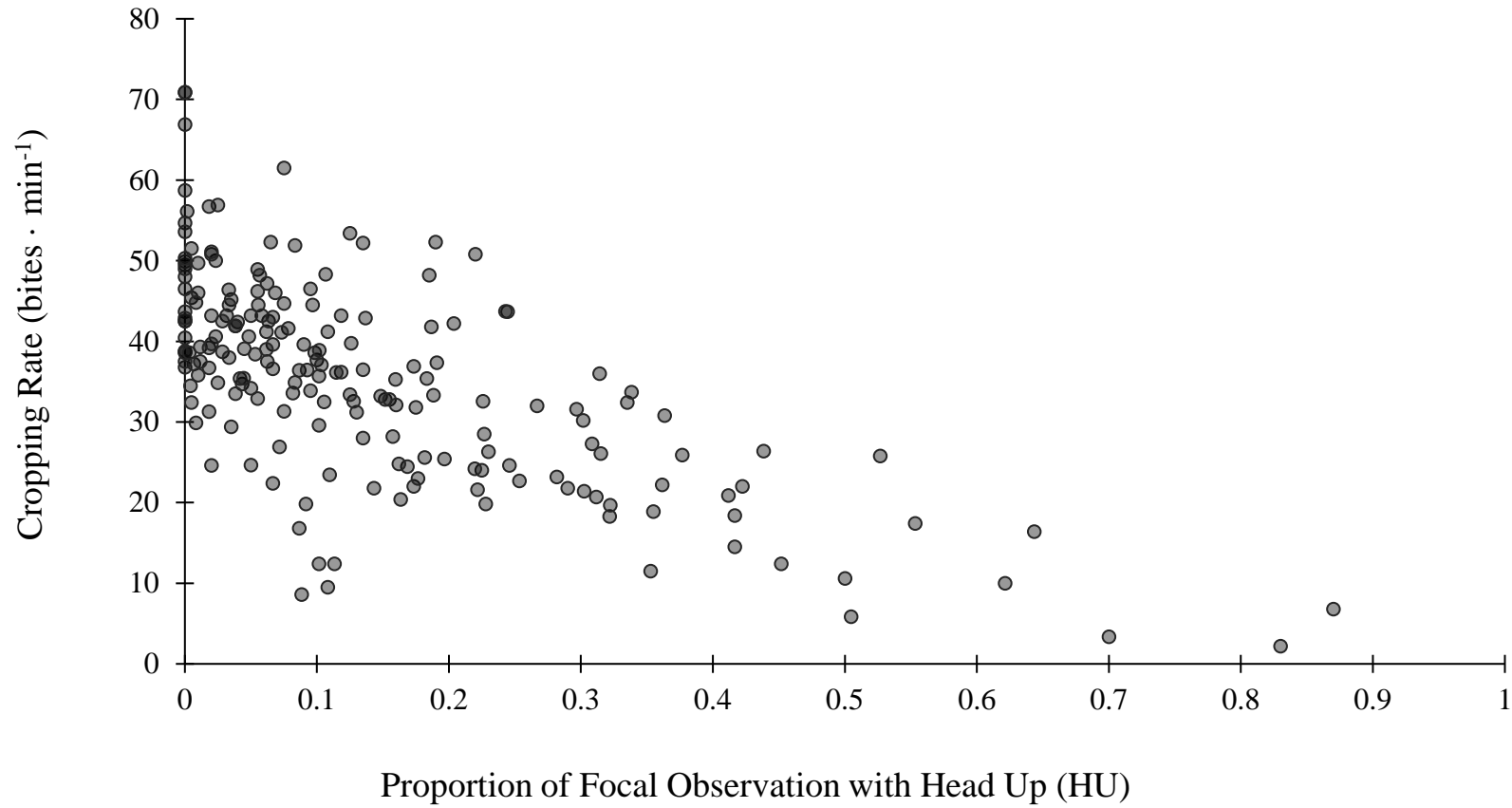
Model fixed effects	$\Delta\text{BIC}$	nPar + nRE	$r_m^2$	$r_c^2$
HU + Prop1BL + minutes + timeprop + sex	0.00	8	0.48	0.58
HU + Prop1BL + minutes + timeprop + sex + biomass	0.59	9	0.49	0.59
<b>HU + Prop1BL + minutes + timeprop</b>	<b>1.92</b>	<b>7</b>	<b>0.47</b>	<b>0.57</b>
HU	9.73	4	0.42	0.54

**Table 3.**—Parameter estimates summarizing three competing linear mixed effects models that predict elk cropping rate. The fixed predictors were proportion of time spent with the head up (HU;  $\beta_1$ ), the proportion of time spent within one body length of a conspecific (1BL;  $\beta_2$ ), length of the focal observation in minutes (m;  $\beta_3$ ), time of day (t;  $\beta_4$ ), elk sex and age class (s;  $\beta_5$ ), and estimated forage biomass (b;  $\beta_6$ ) on cropping rate. Below each beta is its bootstrapped 95% confidence interval.

Model	$\beta_0$	$\beta_1$	$\beta_2$	$\beta_3$	$\beta_4$	$\beta_5$	$\beta_6$	Residual SD
HU + 1BL + m + t	24.68	-49.90	6.42	0.95	0.59	-	-	8.01
	14.87, 34.74	-57.70, -42.39	1.83, 11.62	0.21, 1.69	0.13, 1.09	-	-	7.20, 8.83
HU + 1BL + m + t + s	24.30	-48.31	5.34	1.08	0.60	-3.01	-	7.95
	14.31, 33.55	-56.56, -40.79	0.53, 10.17	0.34, 1.88	0.16, 1.09	-5.65, -0.25	-	7.12, 8.77
HU + 1BL + m + t + s + b	27.96	-48.93	5.23	1.04	0.66	-2.95	-0.01	7.91
	17.08, 39.59	-57.24, -41.37	-0.05, 10.54	0.26, 1.80	0.16 1.11	-5.71, -0.23	-0.04 0.01	7.07, 8.68



**Figure 1.**— The Strategic Compensation Model shows possible relationships between the proportion of a foraging bout spent with the head up (HU) and cropping rate ( $CR_0$  is the cropping rate when HU is 0). The blue line depicts a relationship when cropping rate is constant such that the slope and the y-intercept have the same absolute value. The green shaded area illustrates possible slopes ( $<$  constant) when cropping compensation is occurring. The purple shaded area illustrates possible slopes ( $>$  constant) when no cropping rate compensation occurs. The Incidental Cropping Rate Variability Model shows possible relationships between HU and cropping rate.  $CR_H$  (cropping rate, high) is an example where cropping rate is high when HU is 0 resulting in more food intake over a foraging bout.  $CR_L$  (cropping rate, low) is an example where cropping rate is low when HU is 0 resulting in less food intake over a foraging bout. Intercept values in this model fluctuate, but the slope values are approximately constant because most HU values range between 0 – 0.3 resulting in a slope that is less variable. The red line depicts the relationship between maximum possible cropping rate and HU.



**Figure 2.**—Scatterplot showing the association between the predictor proportion of a focal observation spent with the head up (HU) and the response variable cropping rate of Roosevelt elk during 199 focal observations. When HU is the only fixed effects predictor of cropping rate, the marginal  $r^2 = 0.42$  and the condition  $r^2 = 0.54$ .

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