When can cropping rate compensate for increased vigilance?

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Abstract
Herbivores use vigilance to reduce predation risk and interact socially, yet it imposes a foraging efficiency cost. As individuals spend more time with their head up being vigilant, time available to search for and ingest food decreases. We explored whether ungulates can strategically modify behaviours to compensate for vigilance costs via increased cropping rate when food searching time was near-zero and bite sizes were small. We compared the proportion of time individuals had their head up to their cropping rate (bites/observation length) in 271 observations of Roosevelt elk (*Cervus elaphus roosevelti*). Using a linear mixed-effect model, we estimated the head up–cropping rate relationship and found that elk cropping rate was constant across varying lengths of time spent with their head up, indicating no vigilance compensation occurred via increased cropping rate. We discuss settings when cropping rate compensation is expected and other behaviours that might mitigate vigilance costs.

Keywords
vigilance, *Cervus elaphus*, forage intake rate.

1. Introduction
Vigilance is an antipredator and social behaviour characterized by heightened alertness and is used to detect and monitor stimuli including the presence of predators, competitors, and behaviours of conspecifics (Boggs, 1992; Bednekoff & Lima, 1998; Treves, 2000; Beauchamp, 2015; Tatte et al., 2019). Vigilance is essential to informing an animal about dangers in its environment. For example, Thomson’s gazelles (*Eudorcas thomsonii*) that spend less time vigilant are more likely to be hunted by cheetahs (*Acinonyx*...
*jubatus* than their vigilant counterparts (Fitzgibbon, 1989). Despite its clear advantages, time spent vigilant directly detracts from time available to search for and consume forage, and therefore may reduce food intake (Underwood, 1982; Houston et al., 1993; Fortin et al., 2004b; Creel et al., 2007; Djagoun et al., 2013; Robinson & Merrill, 2013) and directly impact resource selection, organism life-history patterns, energy transfer through the food chain, and subsequently population ecology (Boggs, 1992; Parker et al., 1996; Brown et al., 1999). To combat the consequences of increased vigilance, it is possible that ungulates such as Roosevelt elk (*Cervus elaphus roosevelti*) strategically modify their foraging behaviours to increase their food intake while foraging. In this study, we attempt to answer the question: can elk compensate for the costs of vigilance by modifying their cropping rate while foraging?

Few studies examine if ungulates modify foraging rate deliberately to compensate for vigilance-imposed costs. The idea of “spare capacity” or “spare time” speculates that herbivores might be capable of maintaining their rate of food intake despite being highly vigilant because of their ability to scan the environment while simultaneously chewing forage (Illius & Fitzgibbon, 1994; Fortin et al., 2004a). Food processing by chewing and swallowing constitutes a substantial proportion of foraging time, particularly when animals take big bites (Blanchard & Fritz, 2007; Dannock et al., 2019). Consequently, the ability to combine the time needed for chewing and processing forage with a vigilant period can increase forage efficiency. Even so, the practical applications of spare capacity may be limited when we consider that spare capacity may not be needed in environments where available forage is easily masticated and requires little chewing time before being swallowed (Weckerly, 2017). Furthermore, when an ungulate detects threatening stimuli, they tend to focus solely on the stimulus without chewing at all (Dannock et al., 2019), perhaps because chewing is loud and can jostle an animal’s field of vision, conceivably interfering with predator detection (Blanchard & Fritz, 2007).

Using Roosevelt elk as our study system, we investigated an alternative behavioural modification that ungulates might use to decrease vigilance costs and increase foraging efficiency: increased cropping rate. As the proportion of time spent vigilant while foraging increases, elk might strategically increase their cropping rate (bites per unit time), effectively increasing instantaneous intake rate during the foraging period and offsetting some of
Figure 1. Possible relationships between the proportion of a foraging bout spent with the head up (HU) and cropping rate. CR₀ 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 red function depicts the relationship between maximum possible cropping rate and HU. The green shaded area illustrates possible slopes (>constant, <maximum) when cropping compensation is occurring. The purple shaded area illustrates possible slopes (<constant) when no cropping rate compensation occurs.

the cost of lost foraging time due to increased vigilance (Figure 1). Elk are a sexually dimorphic grazing species that adjust vigilance and foraging levels in response to social factors including group size and group sex composition (Peterson & Weckerly, 2017), predator presence (Laundre et al., 2001), and individual body condition (Laundre et al., 2001; Winnie & Creel, 2007). Elk dominance hierarchies dictate much of their social interactions; less dominant individuals such as females and juveniles increase vigilance in the presence of their dominant male counterparts, presumably to avoid potentially aggressive interactions (Weckerly et al., 2001). Mother elk foraging with their offspring also increase vigilance levels as their perceived predation risk increases (Laundre et al., 2001). Additionally, elk in Yellowstone showed markedly increased vigilance following the reintroduction of wolves (Canis lupus) to the park, demonstrating their sensitivity to predator presence (Laundre et al., 2001). These examples demonstrate the complex nature of foraging and vigilance behaviours.

Forage intake is the product of bite rate and bite size. Foraging dynamics dictate that two conditions must be met for compensation via increased crop-
ping rate to be possible: one, bite sizes must be relatively small to increase the rate at which bites are chewed and swallowed and thus minimize the competition between cropping and chewing and (Spalinger & Hobbs, 1992), two, there must be forage saturation to reduce the time used searching for forage and thus minimizing competition between cropping and food searching (Illius & Fitzgibbon, 1994). These two conditions are expected when available forage is young with low fibre content and carpets a habitat such as a grassland. The low forage biomass of young, short grasses and forbs coupled with their tender forage tissue results in small bites that can be swallowed or readily masticated, thus mitigating chewing from impeding cropping (Greaves, 1978). Forage that carpets a habitat presents abundant bites, reduces food searching time, and competition between cropping and chewing (Greaves, 1978; Weckerly, 2017). Elk foraging in meadows in north-coastal California, USA, in early winter satisfy both conditions. In our study area, over 95% of forage biomass estimates were between 250 and 300 kg/ha in early winter, which is considered low (Weckerly, 2017: Fig. 3.1). At these small forage biomasses, bite sizes are small (0.025–0.15 g) (Wickstrom et al., 1984), and the availability of big bites (>0.5 g) that can cause competition between cropping and chewing is greatly reduced (Spalinger & Hobbs, 1992; Bradbury et al., 1996). Despite the low forage biomass, meadows were carpeted by young shoots of grasses and forbs which reduced an elk’s need to search for food and, thus, reduced competition between cropping and food searching (Bradbury et al., 1996). In this setting, strategic adjustment of cropping rate might yield greater energy intake for elk compared to seeking bigger bites to crop (Figure A1 in the Appendix; see also Weckerly, 2017).

The potential relationships between vigilance and cropping rate are depicted in Figure 1. The maximum possible cropping rate (bites per unit time), illustrated as the red function, depicts a scenario in which forage is saturated, cropping is minimally impeded by chewing, and thereby the fastest possible cropping rate is constrained only by the physical limitations of the animal. If cropping rate is constant across a range of proportions of time the head is up, i.e., vigilance behaviour, then the absolute value of the slope of the relationship will be equal to the cropping rate when the head is down for the entire foraging period (intercept coefficient labelled CR0) as illustrated by the blue function in Figure 1. If cropping rate compensation is occurring, then we can expect the slope of the relationship to have an absolute value
greater than the cropping rate when the head is down for the entire foraging period. If cropping rate compensation is not possible, cropping rate over the foraging period might decrease more rapidly as the proportion of a focal observation spent with the head up (HU) increases (purple shaded area). To investigate the possibility of cropping rate compensation, we observed free-ranging Roosevelt elk as they foraged, recording the proportion of time they spent vigilant and cropping rate. We present and test a novel model to examine how herbivorous ungulates might mitigate the costs of vigilance.

2. Materials and methods

2.1. Study area

Our study was in the Prairie Creek drainage of Redwood National and State Parks, California (41°24′N, 124°02′W). The study area was made up of two meadow complexes within a larger forested landscape (Weckerly, 2017). Coastal redwood (Sequoia sempervirens), Douglas-fir (Pseudotsuga menziesii), Sitka spruce (Picea sitchensis), and Western hemlock (Tsuga heterophylla) were among the most abundant tree species in the study area. Boyes meadow complex is 70 ha in size and Davison meadow complex lies approximately two km away and is 51 ha in size (Peterson & Weckerly, 2017). The meadow complexes had flat terrain and were dominated by annual and perennial grass species such as California oatgrass (Danthonia californica), redtop (Agrostis gigantean), soft chess (Bromus hordeaceus), and reed canary grass (Phalaris arundinacea) (Weckerly et al., 2001; Starns et al., 2015). This region of California has cool summers (seldom above 10°C), rainy and mild winters (3–5°C), and an annual precipitation greater than 150 cm, with rainfall most prevalent from fall to early spring (Starns et al., 2015). The primary predators of elk in the area are black bears (Ursus americanus) and mountain lions (Puma concolor), with occasional predation by coyote (Canis latrans) and bobcat (Lynx rufus) (Bowyer, 1981). Predator pressure was marginal during the observation periods because observations were collected during daylight hours in January. Black bears mainly predate elk calves, rarely hunting adult elk, and so presented little predation risk as calves born in the spring were nearly adult sized by January. Additionally, mountain lions are nocturnal hunters, decreasing the likelihood they presented hunting pressure during the daytime observational periods. Elk in the Prairie Creek drainage are habituated to the presence of humans, as park visitors regularly view
these elk at distances of 10 to 500 m. Their tolerance of humans allowed us to observe the elk from close distances without interrupting their normal foraging and vigilance behaviours.

2.2. Data collection

Foraging and vigilance behaviours of elk were measured via focal observation from 2008 to 2012 in January of each year. All visual observations of grazing elk were collected between 50 and 200 m away from the individual being observed. Most elk were unmarked and indistinguishable from others, so focal elk were chosen randomly. Focal observations were conducted on individual elk that were foraging using digital voice recorders to record observations that ranged from 4 to 15 min in length with 90% of observations falling between 4 and 10 min. A focal observation terminated when the focal elk was no longer visible for observation. The start and end times when the focal elk lifted its head above its shoulders (head is up and therefore the animal is neither feeding nor food searching) were recorded to calculate the proportion of time the animal spent vigilant on a per-minute basis (Favreau et al., 2015; Peterson & Weckerly, 2018; Dannock et al., 2019). Bites taken were counted during the focal observation and cropping rate was (the number of bites taken)/(focal observation length). Sex, age class of the focal elk, and group type (male in a male-only group, females in female group, male in female group, and juveniles in female group) were recorded to capture any potential influences these factors might have on cropping rate (Townsend & Bailey, 1981; Weckerly, 2001; Peterson & Weckerly, 2017). Males were included in two group types to assess if their behaviours varied when grouped with females because males are socially dominant to females. Chewing rate ((number of chews)/(focal observation length)), length of focal observation, group size, date, and sector (part of meadow) where the focal animals foraged were also recorded.

Available forage biomass was estimated each January from 2008 to 2012 in 570 0.25-m² plots measured in 10 sectors in the two meadow complexes (Weckerly, 2017). Delineating sectors ensured that all parts of meadow complexes were sampled. In each sector, 10–40 0.25-m² 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). From 2005 to 2007, clippings from 129 randomly chosen plots were collected, sorted by type...
(grasses, forbs, or shrubs), dried, and then weighed to the nearest 0.1 g. Multiple regressions using plant heights and coverage predicted dried biomass of grasses, forbs, and shrubs. These two regressions were then used to estimate biomass from average height and coverage measurements taken in each of the 570 plots.

2.3. Analysis

Individual focal elk were likely observed on more than one occasion because most elk were untagged and thus indistinguishable from one another (Peterson & Weckerly, 2018). To account for inability in the field to observe all elk and the possibility that some elk were observed more than once, a linear mixed-effect model was estimated using the random factor Julian date to accommodate the possibility of measuring elk multiple times (Bates et al., 2015). Cropping rate ((number of bites)/(focal observation length)) was the response variable. The fixed effect predictors of cropping rate were proportion of focal observation with head up, group type (indicating sex and age class of forager), chewing rate, available forage biomass, total length of time of focal observation, and group size. The random factors were year of data collection, sector, and day of focal observation coded to year and Julian date (e.g., 5 January 2009 was five09) (Peterson & Weckerly, 2018; McGuire & Weckerly, 2020). Each random factor had an intercepts random effect. Using a parametric bootstrap, we calculated the 95% confidence intervals of the fixed and random intercept estimates of the model. The model was bootstrapped 1000 times and estimated using the lme4 package in program R version 4.0 (R Core Team, 2020).

3. Results

Of the 271 observations, 121 were of female elk, 27 were of male elk foraging with females, 73 were of male elk foraging in male-only groups, and 50 were of juveniles foraging in female groups. The mean elk cropping rate was 36 bites/min with a minimum of 3 bites/min and a maximum of 62 bites/min (Table 1). The mean proportion of time the head was up was 0.12 (min: 0.00, max: 0.95), mean chewing rate was 5 chews/min (min: 0 chews/min, max: 18 chews/min), mean group size was 25 elk (min: 1 elk, max: 55 elk), and mean forage biomass was 291.60 kg/ha (min: 112 kg/ha, max: 291.60 kg/ha) (Table 1). The proportion of time with the head up
Table 1.
Summary of cropping rate (bites/min), proportion of time with head up, focal observation length (min), group size, forage biomass (kg/ha), and chewing rate (chews/min) ($N = 271$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Minimum</th>
<th>Quartiles</th>
<th>Maximum</th>
<th>Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>First</td>
<td>Second</td>
<td>Third</td>
</tr>
<tr>
<td>Cropping rate</td>
<td>2.50</td>
<td>30.24</td>
<td>35.46</td>
<td>41.50</td>
</tr>
<tr>
<td>Head up</td>
<td>0.00</td>
<td>0.031</td>
<td>0.080</td>
<td>0.16</td>
</tr>
<tr>
<td>Focal observation</td>
<td>3.23</td>
<td>4.89</td>
<td>5.58</td>
<td>8.15</td>
</tr>
<tr>
<td>Group size</td>
<td>1.00</td>
<td>5.00</td>
<td>33.00</td>
<td>35.00</td>
</tr>
<tr>
<td>Forage biomass</td>
<td>112.00</td>
<td>159.20</td>
<td>285.20</td>
<td>330.60</td>
</tr>
<tr>
<td>Chewing rate</td>
<td>0.00</td>
<td>2.90</td>
<td>4.67</td>
<td>7.29</td>
</tr>
</tbody>
</table>

was the only predictor that influenced the response variable cropping rate (Table 2). The average proportion of time spent with the head up of 0.12 coincided with proportions observed in previous studies measuring elk vigilance rates (Laundre et al., 2001; Childress & Lung, 2003). The model estimated

Table 2.
Parameter estimates, standard deviations of random effects, residual standard deviation, and parametric bootstrapped 95% confidence intervals from linear mixed-effect model ($N = 271$) predicting cropping rate of focal elk.

<table>
<thead>
<tr>
<th>Fixed predictor</th>
<th>Estimate</th>
<th>Lower bound</th>
<th>Upper bound</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>39.793</td>
<td>31.137</td>
<td>48.144</td>
</tr>
<tr>
<td><em>Head up proportion</em></td>
<td>−40.613</td>
<td>−47.288</td>
<td>−33.700</td>
</tr>
<tr>
<td>Total time of observation</td>
<td>0.125</td>
<td>−0.400</td>
<td>0.644</td>
</tr>
<tr>
<td>Female in female group</td>
<td>0.909</td>
<td>−1.741</td>
<td>3.417</td>
</tr>
<tr>
<td>Male in female group</td>
<td>2.401</td>
<td>−0.508</td>
<td>5.375</td>
</tr>
<tr>
<td>Male in male-only group</td>
<td>−0.744</td>
<td>−6.429</td>
<td>4.893</td>
</tr>
<tr>
<td>Group size</td>
<td>−0.152</td>
<td>−0.330</td>
<td>0.027</td>
</tr>
<tr>
<td>Forage biomass</td>
<td>0.012</td>
<td>−0.004</td>
<td>0.028</td>
</tr>
<tr>
<td>Chewing rate</td>
<td>0.031</td>
<td>−0.257</td>
<td>0.351</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Random effects and residual</th>
<th>Standard deviation</th>
<th>Lower bound</th>
<th>Upper bound</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day</td>
<td>3.907</td>
<td>2.397</td>
<td>5.346</td>
</tr>
<tr>
<td>Sector</td>
<td>3.724</td>
<td>1.021</td>
<td>6.177</td>
</tr>
<tr>
<td>Year</td>
<td>0.519</td>
<td>0.000</td>
<td>2.694</td>
</tr>
<tr>
<td>Residual</td>
<td>5.711</td>
<td>5.164</td>
<td>6.28</td>
</tr>
</tbody>
</table>

Group type reference category was juvenile in female group. Italics signifies fixed predictor that influenced cropping rate ($p < 0.05$).
that while the head was down 100% of the time during a focal observation (CR₀, Figure 1) the cropping rate was approximately 40 bites/min with a bootstrapped 95% confidence interval of 31–48 bites/min (Table 2). The slope of the regression was similar in absolute value to the intercept and was −40 bites/min (95% CI = [−46, −35]). The relationship between HU and cropping rate fit the observed data well (Figure 2). Day and sector tended to be more heterogeneous than year. Moreover, the standard deviations for day and sector were similar to the residual standard deviation.

4. Discussion

Our study is the first to examine whether ungulates strategically alter cropping rate to offset lost foraging time due to vigilance. However, we found that cropping rate did not change across a wide range of proportions of time a focal elk spent with its head up, indicating that there was no vigilance compensation via increased cropping rate.

We failed to detect cropping rate compensation although environmental conditions in the RNSP in January were seemingly favourable to detecting compensation. Firstly, the estimated average cropping rate of 40 bites/min

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**Figure 2.** Scatterplot showing proportion of focal observation spent with the head up versus cropping rate (bites/min) of Roosevelt elk with predicted relationship from linear mixed effect model (N = 271).
when HU is zero is well below the maximum possible elk cropping rate of 83.3 bites/min reported by Gross et al. (1993). The slower cropping rate estimated in our study indicated that there was opportunity for elk to increase cropping rate. If our estimated cropping rate was near the maximum possible cropping rate, the range of compensation for elk would be much more limited. Secondly, elk chewing rate does not interfere with their cropping rate in January (Weckerly, 2017). Available forage biomass ranged between 100–500 kg/ha which is low across the spectrum of forage biomasses encountered by elk in grasslands (100–7000 kg/ha (Weckerly, 2017: Fig. 3.3)). When biomass is <500 kg/ha elk bite sizes are likely to be <0.2 g (Weckerly, 2017). Bite sizes in our study are probably small as elk bite sizes can be as large as 2.5 g and often are greater than 0.25 g (Gross et al., 1993; Cook et al., 2016). Chewing and cropping can be competing processes when bite sizes are large because animals take more time to comminute ingested plant tissue before swallowing which reduces time available for cropping. Another bit of evidence to indicate that elk in January were taking small bite sizes is the bites:chew ratio. On average, the bites:chew ratio was about 7 in our study (Table 1). When larger bites are taken the bites:chew ratio becomes smaller as more comminution of large bites is required. From studies of giraffe (*Giraffa camelopardalis*), moose (*Alces alces*), and another study of elk, where bite sizes averaged 0.35 g or larger, the bites:chew ratio ranged from 0.33 to 3.7 (Gross et al., 1993; Ginnett & Demment, 1995; Pastor et al., 1999; Nordengren & Ball, 2005). That range of ratios was noticeably smaller than our estimated ratio. Notwithstanding different body sizes and forages, the smaller ratios with large bite sizes in those studies is consistent with our supposition that elk in our study took small bites. As such, the low available forage biomass in this study should have been a favourable condition for detecting cropping rate compensation because when elk crop small bite sizes, they should have the opportunity to compensate for HU by cropping bites faster. Additionally, forage in the RNSP in January is young and green (Weckerly, 2017). The lack of fibrousness of the young forage decreases the need for extensive chewing before swallowing ingesta. Thirdly, the dense ground of short grasses and forbs with little bare ground (Weckerly, 2017: Figure 0.1, 0.2) reduces time needed to search for bites and should have further enabled compensation by increased cropping rate. As forage density increases, food searching decreases, allowing elk to increase their cropping rate. When forage is effectively saturated,
the relationship between forage density and cropping rate becomes asymptotic and further forage density increases no longer influence cropping rate because searching time is already near its lowest possible value (Bradbury et al., 1996). Forage saturation in our study is possibly evidenced by the lack of influence biomass had on predicting cropping rate (Table 2).

Assessing the non-influential predictors in our model might illuminate possible avenues for improving the model and help guide future investigations. Group type, group size, length of focal observation, and available forage biomass did not have a significant effect on cropping rate, though previous studies show these factors can influence forage behaviours (Miquelle et al., 1992; Weckerly et al., 2001; Peterson & Weckerly, 2018). Group type might not have influenced cropping rate because males and females often differ in HU time (Peterson & Weckerly, 2018). Consequently, if HU was eliminated from our model, we likely would have detected differences in cropping rates across group types. Across the range of group sizes in this study, individual elk might be more responsive to group density or the time spent in close proximity to conspecifics (Peterson & Weckerly, 2018). Possibly, length of time of focal observation did not influence cropping rate because the bulk of focal observations might have been too short. Elk forage for an estimated 45–55% of each day in bouts that tend to last 2–4 h (Cook et al., 2016; Roberts et al., 2017), and compensation through increased cropping rate might only be detected when a longer proportion of foraging bouts are measured. Biomass did not influence cropping rate despite the two-fold range in available forage biomass. Available forage biomass at the scale of the sector might not reflect forage biomass at the spatial scale along the forage path of an elk (Weckerly, 2017). As mentioned previously, it might also indicate forage saturation.

The data for our analysis was collected under conditions that should have allowed us to detect cropping rate compensation if it occurred. There might have been additional variables not discussed above that might have influenced HU–cropping rate relationships. An indication that there might be additional variables can be gleaned by considering the heterogeneity captured by our random effects. Time of day that the focal observation was measured might be one such predictor (Peterson & Weckerly, 2017). Elk in the Pacific Northwest can be bedded and inactive much of the night (Cook et al., 2016; Weckerly, 2017) which might affect patterns of day time foraging. Grazing elk in winter in this population have been shown to vary HU and
tortuosity of the forage path with time of day (Peterson & Weckerly, 2018). A more rigorous test might consider these predictors.

It is plausible that the cropping rate compensation model is incorrect for capturing how elk might mitigate costs imposed on foraging. The model can be described from a statistical view as invariant intercept with adjustments in slopes. Possibly, foraging elk respond to vigilance by adjustments in the intercept but not the slope. Increases in the intercept with the same slope, as an example, might return greater food intake then adjustments in slopes and an invariant intercept, particularly if vigilance does not take up a lot of foraging time. It would be informative to conduct rigorous tests of these competing models to determine whether ungulates can strategically alter foraging behaviour to mitigate the costs of vigilance on foraging.

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References


Figure A1. Line graph illustrating relative percent change in food intake to percentage change in forage biomass or cropping rate. Predicted forage intake was the product of bite size and cropping rate. Bite size was predicted from the equation presented in Weckerly (2017, bite size = 0.0026 × Forage biomass 0.63) which was estimated from 59 data points gathered from eight studies. Relative percent change was estimated as \( \frac{(\text{FI}_{\text{max}} - \text{FI}_{\text{min}})}{\text{FI}_{\text{min}}} \times 100 \) \( \frac{(R_{\text{max}} - R_{\text{min}})}{R_{\text{min}}} \times 100 \) where FI is food intake and R is either forage biomass or cropping rate. Range in forage biomass was determined from forage biomass estimated in Davison meadows in January from 2005 to 2016 (Weckerly, 2017: Fig. 3.2). Range in cropping rates was determined from measured cropping rates of Roosevelt elk in January and the highest predicted cropping rate of 83 bites/min in Gross et al. (1993).