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GRAZING IN HERDS: WHEN ARE NUTRITIONAL BENEFITS REALIZED?

McNaughton (1984) showed that feeding in groups can convey significant nutritional benefits to large herbivores by enhancing food yield from the grasslands they feed upon. However, the nutritional benefit of gregarious behavior was subsequently questioned by Westoby (1985), who reviewed empirical evidence showing that increases in herbivore density frequently compel deterioration in their nutritional status. McNaughton (1986) argued that this discrepancy was due to differences in the evolutionary history of domestic and wild grazers. We believe there is a more parsimonious explanation. Here, we offer a simple model that reconciles the seemingly conflicting observations of Westoby and McNaughton, showing them to be specific examples of a more general case.

Gregariousness is nutritionally advantageous when the capture of nutrients by herbivores feeding in grazed patches exceeds nutrient capture in ungrazed patches (McNaughton 1986). The expected rate of nutrient intake from grazed and ungrazed patches can be predicted from the functional response of the herbivore, the standing crop of the grazed and ungrazed patches, and the difference in nutrient concentrations of the grazed and ungrazed forage. The rate of nutrient intake (F , in g/min) by a feeding herbivore is a product of its dry-matter intake rate (I , in g/min) and the concentration of nutrients (D , a decimal fraction) in the mass of forage eaten: $F = ID$. The dry-matter intake rate of large herbivores is an asymptotically increasing function of the mass of available forage (Allden 1962; Allden and Whittaker 1970; Wickstrom et al. 1984; Short 1985, 1986; Hudson and Watkins 1986; Renecker and Hudson 1986), which can be represented in the form $I = ax/(b + x)$, where x is the standing crop of food; a is a constant describing the maximum intake rate; and b is a constant describing the rate of approach to maximum intake.

Assuming that the standing crop of ungrazed grass exceeds the standing crop of regrowth in a grazed patch, the biomass of regrowth (R , in kg) following grazing can be expressed as a fraction (f_1) of the original, ungrazed biomass (U , in kg): $R = f_1 U$, where $0.0 < f_1 < 1.0$. Similarly, the concentration of a nutrient in regrowth (D_g) can be expected to exceed its concentration in mature, ungrazed forage (D_u). It follows that the nutrient content of regrowth can be expressed as a multiple (f_2) of the nutrient content of mature forage: $D_g = f_2 D_u$, where $f_2 > 1.0$. The expected intake of nutrients in grazed (F_g) and ungrazed (F_u) food patches can then be calculated as a function of the standing-crop biomass and of the nutrient concentration of the ungrazed food:

$$F_u = aUD_u/(b + U);$$

$$F_g = af_1UD_uf_2/(b + f_1U).$$

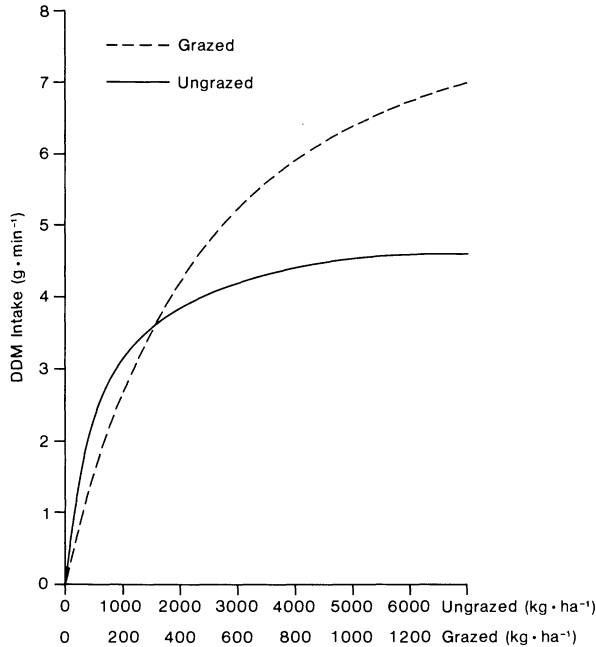


FIG. 1.—The expected intake rate of digestible dry matter (DDM) of elk feeding in grazed and ungrazed grasslands. Grazed forage biomass is assumed to be 20% of ungrazed biomass.

Some example data from elk (*Cervus elaphus nelsoni*) feeding in temperate grasslands can be used to illustrate graphically an important general outcome of the model. Phenologically young grass in elk diets is roughly twice as digestible as mature or senescent grass (about 70% vs. 35%; Hobbs et al. 1981; Baker and Hobbs 1982). The functional response of elk feeding in grasslands is given by $I = 14.04x/(541.8 + x)$ (Wickstrom et al. 1984). Assume for the purpose of illustration that the biomass of patches of regrowth is about 20% of the biomass of the ungrazed standing crop. Under these conditions, the capture rate of digestible dry matter by elk feeding in grazed and ungrazed grasslands is given in figure 1.

When biomass of the ungrazed standing crop is large (> 1625 kg/ha), the result predicted by McNaughton (1984) is obtained: the rate of digestible dry-matter intake by elk is greater when feeding on regrowth than when eating ungrazed, mature forage. When the biomass of the ungrazed plant community is low (< 1625 kg/ha), the expectation is consistent with the observations of Westoby (1985): the capture rate of digestible forage is greater in the ungrazed patch, despite the higher nutritional value of regrowth.

The specifics of these curves do, of course, depend on the functional response of the herbivore in question, the values of f_1 and f_2 , and the nutrient chosen as the currency in the analysis. However, the important conclusions here depend not on the details of the curves, but on the fact that they intersect such that feeding in grazed patches is nutritionally beneficial in systems with high forage biomass and nutritionally detrimental in systems with low forage biomass. It can be shown (see

the Appendix) that the biomass at which the curves cross (U_i) is given by

$$U_i = b(f_1 f_2 - 1)/f_1(1 - f_2).$$

It follows that the grazed and ungrazed curves intersect at positive values of forage biomass whenever $1/f_1 > f_2$, that is, whenever the difference between the grazed and ungrazed biomass is proportionately greater than the difference in grazed and ungrazed nutrient concentrations. This is frequently the case. For example, the standing crop of ungrazed grasslands in the Serengeti is 2.5–5.0 times as great as the standing crop of regrowth patches following grazing by wildebeest, but the nitrogen concentration of regrowth patches differs from that of ungrazed patches by a factor of only 1.4 (McNaughton 1985, pp. 274–275). Young grass is usually no more than twice as digestible as mature grass (Van Soest 1982, figs. 5.3, 5.4).

When $1/f_1 \leq f_2$, nutrient intake rate of herbivores feeding in grazed patches always exceeds the rate in ungrazed ones. Under these circumstances, the standing mass of nutrients in grazed patches is equal to or greater than the mass of nutrients in ungrazed patches, but the concentration of nutrients is greater in the forage of grazed patches.

Where the two curves intersect, the instantaneous rates of nutrient intake are equal. However, a nutritional advantage may occur at this point for ruminant herbivores grazing the higher-quality forage. On low-quality diets, total daily intake by ruminants may be limited by the rate of passage of ingesta from the rumen (Thornton and Minson 1973; Baile and Forbes 1974; Baker and Hobbs 1987). When this is the case, animals can respond to improved forage quality by increasing intake (Montgomery and Baumgardt 1965; Ammann et al. 1973; Lippke 1986). Thus, when instantaneous intake rates are equal for two ruminants, the animal consuming the higher-quality diet may be able to increase its daily intake (and, hence, its nutrient capture) if it can also increase its daily foraging time. However, the time available for foraging may be constrained by thermoregulation, predator avoidance, or caring for young. In the face of such constraints, animals with higher instantaneous intake rates will probably have higher daily intake rates.

The model illustrates that stimulation of the rate of plant growth in response to grazing ("compensation"; McNaughton 1979, 1983, 1985; Hilbert et al. 1981; Coppock et al. 1983a; Wallace et al. 1984, 1985; Belsky 1986; Page and Whitham 1987) is neither a necessary nor a sufficient condition for enhancing herbivore nutrition in grazed patches ("facilitation"; Bell 1971; Jarman 1974; McNaughton 1976, 1984; Coppock et al. 1983b). It is unnecessary because the nutrient capture rate can be elevated without a stimulation of plant growth whenever grazing-induced increases in forage quality (f_2) are large enough to offset the effects of a reduced standing crop ($1/f_2 \leq f_1$). It is insufficient because an herbivore with an intake rate sensitive to changes in the standing crop over a broad range of biomass (an herbivore with a relatively large b in its functional response) may be unable to benefit from increases in the rate of food yield because of reductions in its instantaneous mass. If all other parameters are held constant, increasing b results in intersections (U_i) at higher biomass values, thereby reducing the range of conditions where an herbivore will benefit from feeding on regrowth.

The predictions of the model are consistent with intuitive expectations. When

food is scarce, nutrient capture rate is limited by food amount and its effects on dry-matter intake rate. When food is more plentiful, however, nutrient capture is more strongly influenced by food quality because the intake rate of herbivores is independent of forage biomass when the standing crop is large, but it can be strongly influenced by that biomass when the standing crop is small (Allden 1962; Allden and Whittaker 1970; Wickstrom et al. 1984; Short 1985, 1986; Hudson and Watkins 1986; Renecker and Hudson 1986).

The observations of McNaughton (1984) were drawn from a relatively productive tropical system. Westoby's (1985) view was influenced by semiarid, less productive ones. Productive systems offer nutritional benefits to gregarious grazers. Unproductive ones do not.

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APPENDIX

The analytical solution for the value of the ungrazed biomass at the intersection of the grazed and ungrazed curves can be derived as follows:

$$\begin{aligned} aUD_u/(b + U) &= af_1UD_u f_2/(b + f_1 U); \\ 1/(b + U) &= f_1 f_2/(b + f_1 U); \\ f_1 f_2(b + U) &= b + f_1 U; \\ f_1 f_2 b + f_1 f_2 U &= b + f_1 U; \\ f_1 f_2 b - b &= f_1 U - f_1 f_2 U; \\ b(f_1 f_2 - 1) &= U(f_1 - f_1 f_2); \\ U &= b(f_1 f_2 - 1)/(f_1 - f_1 f_2). \end{aligned}$$

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