Ecology, 77(7), 1996, pp. 2237–2255

THE RELATIONSHIP BETWEEN BITE RATE AND LOCAL FORAGE ABUNDANCE IN WILD THOMSON'S GAZELLES[1]

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Abstract. The foraging of female Thomson's gazelles (*Gazella thomsoni*) on shortgrass plains was monitored over one annual cycle in southwestern Kenya. Sward dry green biomasses and protein densities were estimated regularly throughout the study site. Changes in protein densities with season and locale were strongly correlated with underlying changes in grass physiognomy: sward height and dry green bulk biomass density were particularly important and were found to vary inversely. The relationship between bite rates and underlying sward parameters varied with season: gazelle bite rates in the dry season were positively correlated with underlying dry green biomass and protein densities, as predicted by either the Process 1 or Process 2 foraging model of Spalinger and Hobbs. Nonlinear regressions of within-bout bite rates on these model equations significantly explained 21.8 and 23.7% of the dry season variance, respectively. In contrast, bite rates in the early wet season showed significant negative correlations with underlying protein densities: the fit of the within-bout bite rate data to Spalinger and Hobbs' Process 3 model explained 18.4% of the overall variation. The late wet season showed a flat (insignificant) relationship between bite rates and protein levels and was thus intermediate between early wet- and later dry-season patterns. Logistic regression of the type of correlation between bite rate and protein density (positive, flat, negative) on two principal components of grass physiognomy suggested that a component heavily weighting sward height was the major correlate of foraging process, whereas a second major component heavily weighting bulk density and other grass quality measures was less critical. At least during this single annual cycle, shorter swards were associated with Processes 1 or 2, whereas taller swards showed Process 3 foraging. One interpretation of these results is that sward height modulates bite mass, which in turn plays the major role in controlling foraging process. Whether the switching point remains the same in subsequent years or not, the results make it clear that the direction of the bite rate vs. foraging density relationship can change markedly with season, as predicted by the Spalinger and Hobbs models.

Key words: antelopes; functional response; Gazella thomsoni; *herbivores; ruminants; sward height; tropical grasslands.*

INTRODUCTION

As part of a larger study on the settlement and dispersion of foraging Thomson's gazelles, we sought to identify the constraints that underlying sward densities might impose on the bite and intake rates of foraging individuals. There has been much recent discussion of the ways in which mammalian herbivore intakes respond to varying food densities (Belovsky 1984, Hodgson 1985, Hudson and Watkins 1986, Illius and Gordon 1987, Demment and Greenwood 1988, Forbes 1988, Spalinger et al. 1988, Penning et al. 1991, Ungar et al. 1991, Illius et al. 1992, Laca et al. 1992, 1994, Shipley and Spalinger 1992, Gross et al. 1993, Jiang and Hudson 1993, Owen-Smith 1993). The classical intake model for predators hunting particulate prey is Holling's Type II functional response: as prey density increases, predator intakes also rise, but in a decelerating and asymptotic manner (Hassell 1981). This deceleration is due to a trade-off between searching for prey and handling them during and after capture: the more prey a predator must handle, the less time is available for searching. The maximal asymptotic rate in this model is set by the reciprocal of the handling time for each captured prey item, and the rate at which the curve rises to the asymptote depends upon the searching efficiency for prey.

Although many herbivore studies show functional responses of the same shape as the classical model, post-capture handling time is unlikely to be the rate-limiting step because herbivores can often "handle" a mouthful of forage and search for the next bite at the same time (Spalinger and Hobbs 1992). Instead, other trade-offs produce the decelerating curve. Herbivore intake rate is the product of bite mass (wet mass of sward, in grams, taken per bite) and bite rate. Bite mass for grazers usually increases monotonically but in a decelerating manner with increasing forage abundance (Hodgson 1985, Hudson and Watkins 1986, Penning 1986, Demment and Greenwood 1988, Forbes 1988, Burlison et al. 1991, Penning et al. 1991, Ungar et al. 1991, Laca et al. 1992, 1994, Shipley and Spalinger

[1] Manuscript received 3 April 1995; revised 18 September 1995; accepted 24 January 1996.
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1992, Flores et al. 1993); it may remain constant or even decrease with increasing forage density in some browsers (Vivås and Saether 1987, Lundberg and Åström 1990, Vivås et al. 1991, Gross et al. 1993).

Bite density, the potential number of bites per unit area, is usually found to increase with forage density. Were bite density the only factor limiting bite rate, one might then expect bite rates always to increase with forage density. Although bite rate and forage density are sometimes positively correlated, the majority of studies of grazers on cultivated swards exhibit an inverse relationship between bite rate and underlying forage density (Penning et al. 1984, 1991, Hodgson 1985, Hudson and Watkins 1986, Penning 1986, Ungar and Noy-Meir 1988, Ungar et al. 1991, Illius et al. 1992, Shipley and Spalinger 1992, Gross et al. 1993, Laca et al. 1994). This nonintuitive observation was clarified by Spalinger and Hobbs (1992), who contrast three possible relationships between herbivore intake and underlying forage density. In Process 1 conditions, forage is sparsely distributed and difficult to spot. This generates a trade-off between biting and searching. The consequence is a positive relationship between bite rate and underlying forage density with a decelerating approach to an asymptotic bite rate at higher forage values. The asymptotic bite rate is equal to the reciprocal of the minimal time required to make a bite, and the rate at which the curve rises to this asymptote is positively correlated with the maximal foraging velocity of the herbivore and the searching area and/or efficiency. Note that even if bite rate becomes asymptotic at higher forage densities, intake could continue to rise beyond this point if bite mass remains positively correlated with forage density, provided that some other limit, such as maximal buccal volume or chewing rate, does not come into play. Thus, Process 1 will show the deceleration in intake of a Type II functional response, but may not exhibit the asymptote.

Spalinger and Hobbs' Process 2 occurs when forage densities are low, but bites are readily visible to the grazer. Here the trade-off is between moving to the next bite and performing the current bite. This model also generates a positive and asymptotic relationship between bite rate and forage density (as long as bite density is positively correlated with forage density). The asymptotic bite rate still depends upon the minimal time per bite, and the rate at which the asymptote is reached as forage density increases varies only with the maximal foraging velocity. As with Process 1, Process 2 conditions allow a continued rise in intake once asymptotic bite rates are reached, as long as bite mass continues to rise unabated with increasing forage density.

When forage is very abundant and visible, searching and moving are no longer limiting time investments. Instead, the maximum rate at which the herbivore can chew and process a mouthful of food sets the upper limit on its intake rates. Spalinger and Hobbs denote these conditions as Process 3. Most herbivores cannot bite and chew accumulated bites at the same time (although some may intercalate the two actions). If bite mass is high, the buccal cavity fills after a small number of bites and the animal must stop biting to chew and swallow the accumulated forage. This creates the negative relationship between bite rate and bite mass, and between bite rate and forage density, so commonly seen in studies of domestic grazers. Even though bite density may increase with forage density, this is unlikely to affect bite rate under these conditions. Intake, which is the product of bite rate and bite mass, will show a Type II functional response with asymptotic deceleration as forage density increases. The asymptote in this case is equal to the maximum rate at which the forager can chew and process accumulated bites. The rate at which the intake curve approaches this asymptote is inversely related to the minimal time per bite. Thus, unlike Processes 1 and 2, Process 3 intakes will always become asymptotic as forage density increases.

As noted by Spalinger and Hobbs, one might observe shifts from Process 1 to Process 2 to Process 3 conditions as forage abundances increase. There are few studies in the current literature of such shifts for either wild or domestic grazers. Since we see large changes in sward measures both within our study site and between seasons, our data on gazelle foraging ought to provide a reasonable case in which such shifts can be observed and used to test the model predictions of Spalinger and Hobbs. Such an analysis is also important if bite rates are to be studied for other purposes. Shifts in foraging process can lead to reversals in the direction of the correlation between bite rates and forage density; pooling of bite rate data across such a shift can lead to very misleading interpretations. In this monograph we demonstrate such shifts and reversals and identify those sward parameters most tightly associated with process shifts in our study site.

Methods

Study site

The study was conducted on a 528-ha patch of plain situated between the Olare Orok and Ntiakitiak rivers and straddling the boundary between the Koyiaki Group Ranch to the north and east and the Maasai Mara National Reserve on the south and west (Fig. 1). The study site was bounded by tracts of riparian woodland along the east and west, a wooded lugga and the tall swards of the reserve to the south, and a dry rocky zone with scattered bushes to the north. The altitude of the site dropped ≈60 m from the northeast down to the southwest corner. Research on this site began in the second half of the dry season in August 1989, extended through the subsequent rainy season, and ended midway through the subsequent dry season in August of 1990. With an eye to the possibility of different foraging and settlement rules at different scales, we

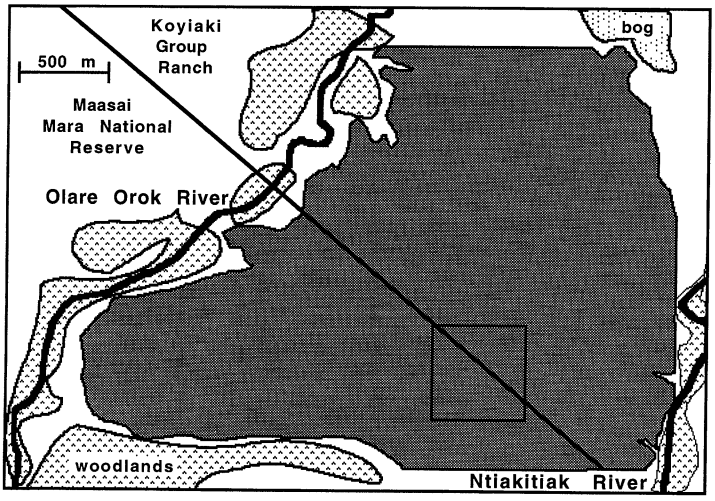

FIG. 1. Map of global study area (shaded) with north at the top of the figure. The dark line running from northwest to southeast is the boundary between Koyiaki Group Ranch and Maasai Mara National Reserve. Altitude ranges from 1600 m (top of study area) down to 1540 m (lower left corner). The square at the lower right indicates the location of the 25-ha central study area. Surrounding woodlands, rivers, and a boggy zone are indicated.

sampled the entire 528-ha area during the first dry season and first half of the rainy season, and then focused on a central 25-ha sub-area for the remaining half of the rainy season and the first half of the next dry season.

The entire study site was grassland habitat dominated by the grass *Themeda triandra.* Throughout most of the area, the grass rarely exceeded 15 cm in height and was more typically 7–8 cm. This was due to regular cropping by Maasai cattle and wild grazers (wildebeest, zebra, topi, impala, and Grant's and Thomson's gazelles). The local Maasai may have burned some of the area prior to our study. The low sward height of the study site contrasted markedly with areas of the reserve west of the Olare Orok River and south of the study site, where the grass routinely reached a height of 1 m or more and wild grazers were much less common (K.E. Clifton, *personal observation*). Wildebeest and zebra were present on the study area in substantial numbers in the dry season, but migrated away during the rainy season. Thomson's gazelles were abundant all year, although densities varied seasonally. Small numbers of topi, Grant's gazelles, and impala were also present on the site throughout the year.

Resource mapping

The amount of plant resources available to the gazelles was estimated radiometrically by simultaneously recording the intensity of two different frequencies of light reflected from the sward (Pearson et al. 1976) and combining the two readings into a single measure, which we call the "vegetation index." It is the convention in the literature to call the relevant instrument a "green machine" (details and component sources in Clifton et al. 1994). Vegetation indices were calibrated using clipped samples taken throughout the study area at frequent intervals. Before clipping, samples were measured radiometrically, and mean sward height and mean blade lengths were recorded. Clipped samples were separated into green (living) and brown (dead) components, weighed, dried, and weighed again to determine percent dry matter. The dried green samples were then analyzed for nitrogen content using Kjeldahl digestion and spectrophotometric quantification (Clifton and Clifton 1991). This allowed the computation of a dry green biomass density and a protein density (both in grams per square metre) for each clipped sample. Measured values for each of these parameters were then regressed on the measured vegetation indices. The log–log regressions for the pooled calibration samples are shown in Fig. 2. Although vegetation indices were more tightly linked to protein densities than to dry green biomass densities, both regressions are remarkably tight. Dry green biomass density is the most commonly used measure of sward quality in the literature (McNaughton 1979, 1985). Because vegetation index is more tightly linked to protein than to dry green biomass densities and because protein is more relevant nutritionally, we use protein density in our subsequent analyses.

Green machine light probes were mounted on a metal bar extending out from the bumper of a Land Rover. The vehicle was outfitted with a computerized navigational system (Navigator Model 450C, Etak Incorporated, Menlo Park, California). The system relies on wheel spin ratios and an electronic compass to estimate location to the nearest 0.1 m (Clifton et al. 1994). Because of a cumulative error of 1–2% with distance traveled, we established a grid of marker poles at 500-m intervals over the entire study area at which known coordinates could be recalled and cumulative error removed. To map the sward resources, we drove the vehicle systematically back and forth across the study plot at speeds of 20–25 km/h. A radiometric measurement was taken every 2 s providing observations $\approx$12 m apart. At the same time, ambient light levels were recorded using a LI-COR photocell (LI-COR, Lincoln, Nebraska). The analog outputs of the green machine and LI-COR probe were digitized using a Remote Mea-

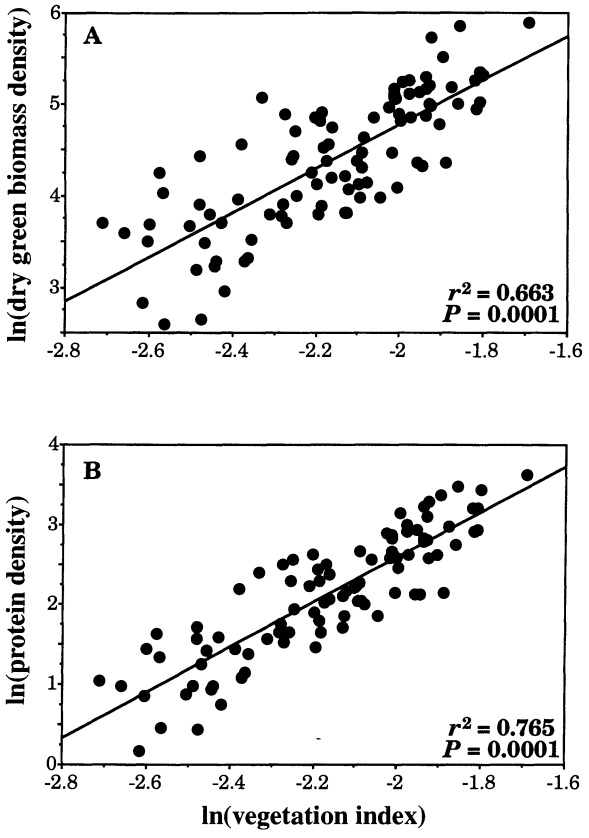

FIG. 2. Relationships between vegetation index and (A) dry green biomass density (g/m^2) and (B) protein density (g/m^2) for the entire study site.

surement Systems ADC-1 (Seattle, Washington) and stored with the corresponding x–y coordinates from the navigator on a Radio Shack Model 100 computer. Using the regressions from concurrently clipped samples, the vegetation indices for each radiometric sample were then converted into protein densities. Green-machine scans of the overall 528-ha study area were undertaken on average every 15 d, and for the 25-ha central area every 5 d.

Resource interpolation

Files containing locations and protein densities were loaded into several custom Macintosh programs (MacPatches and Quadrats, written by the authors), which smoothed the data using quadratic functions and generated cubic spline files (McLain 1974). The smoothing introduced some error at site margins, but comparisons with clipped samples from known locations showed these to be negligible. The spline files were then used to estimate the protein density beneath any given location (e.g., the site of a foraging animal), or to compute the average density and/or total protein within any bounded area. Where estimation was required for a sample taken >2 d later or earlier than a green-machine scan, protein densities were linearly interpolated between the prior and successive spline files.

Gazelle mapping

To map the positions of gazelles on the study site, a second vehicle was outfitted with an Etak navigator and a Wild Heerbrugg 80-cm-base rangefinder (manufactured in Switzerland) mounted on a tripod on the vehicle roof. A 50-cm-base Sokkisha rangefinder (Tokyo, Japan) was mounted on top of the larger one to map animals within 200 m of the vehicle. Both the main axis of the tripod and the range-adjustment knobs of the rangefinders were attached to potentiometers and batteries that provided analog output of their positions. At the push of a single button, a Radio Shack Model 100 computer polled the digitizer for the outputs of the potentiometers and the navigator and used these to compute the absolute x–y coordinates of the focal animal. In addition, several switches on the side of the rangefinder permitted the simultaneous recording of the sex and status (standing or lying) of each gazelle mapped. Using this equipment, a trained observer could sequentially map hundreds of gazelles within a few minutes. Calibrations showed that the rangefinders were accurate to ± 1 m over a range of 100–700 m. We avoided approaching the gazelles closer than 100 m to avoid behavioral perturbation.

Behavioral samples

To obtain data on foraging rates, 10-min behavioral samples were taken on randomly selected adult female gazelles. One observer used the rangefinder apparatus to map the location of the focal animal every minute. The fixes were then combined with a green-machine scan taken within 2 d of the behavioral samples to estimate the protein densities at each of the 10 locations. The resulting 10 values were averaged to produce a mean protein density experienced by the focal animal during its sample. At the same time, another observer used a spotting telescope and an event-recording computer program to note the focal animal's behavioral states and actions. The four alternative states were foraging, standing, lying down, or engaging in "other" nonforaging activities. An animal that kept its head up for 5 s and was not stepping was characterized as "standing"; a moving animal or one with its head down was "foraging." "Lying" animals were usually either ruminating or sleeping. "Other" activities included intra- or intersexual agonistic interactions, mating, grooming, infant care, running, predator inspection, and drinking. Behavioral events included bites, steps, raising of the head (head-ups), and lowering of the head.

Three summary measures of bite rate were computed by the event-recording program. *Gross bite rates* were computed as the total number of bites recorded during the behavioral sample divided by 10 min (the length of the entire sample). The second measure of bite rate,

TABLE 1. Means and standard errors for sward parameters measured on clippings taken from throughout the 528-ha study site during August 1989–August 1990.

Measure	Mean ± 1 SE	Range
1) Wet total biomass (g/m^2)	334.083 ± 22.79	29.5–1159
2) Wet green biomass (g/m^2)	208.295 ± 18.28	14.1–865.9
3) Protein density (g/m^2)	10.97 ± 0.80	1.18–37.52
4) Wet green biomass (mg/cm^3)	2.635 ± 0.192	0.227–8.247
5) Protein density (mg/cm^3)	0.144 ± 0.009	0.019–0.354
6) Dry total biomass (g/m^2)	220.569 ± 16.23	25.11–946.6
7) Dry green biomass (g/m^2)	101.955 ± 7.291	13.4–361.2
8) Dry green biomass ("bulk density," mg/cm^3)	1.303 ± 0.071	0.158–3.184
9) Sward height (cm)	8.82 ± 0.65	1.8–30.2
10) Lamina length (cm)	5.87 ± 0.29	1.83–17.73
11) Fraction green (by mass) in wet samples	0.610 ± 0.026	0.148–0.965
12) Fraction water in green samples	0.420 ± 0.184	0.0–0.716
13) Fraction protein in dry green moiety	0.107 ± 0.002	0.057–0.164

referred to as *bites/min foraging,* was computed by dividing the total number of bites recorded in the sample by the total number of minutes the animal was in a foraging state. Finally, *within-bout bite rates* were computed by dividing the total number of bites recorded in the sample by the pooled durations of all foraging bouts noted during the sample. (A bout of foraging began when an animal took a first bite and continued as long as the animal did not raise its head and no longer than 5 s passed between bites). Gross rates are the lowest values, because they include time spent on activities other than foraging; within-bout rates are the highest, and are a reasonable measure of the maximum or instantaneous rates on that sward.

In addition to bite rates, two measures of step rate were taken: *gross step rate* was the total number of steps divided by the total sample time, and *steps/min foraging* was the total number of steps taken minus those associated with "other" activities, divided by the pooled durations of foraging bouts. Corresponding velocities were computed as the product of step rates and an average step length (measured from videos) of 0.28 m/step. The joint locational and behavioral samples thus provided a mean underlying protein density, three different measures of mean bite rate, and two measures of velocity for each focal animal. No direct measures of bite mass were undertaken in this study.

Statistical analyses

All results were analyzed on Macintosh computers using either our own custom software or standard commercial programs. Nonlinear regressions followed protocols summarized by Motulsky and Ransnas (1987). Variables were transformed when necessary to meet normality and homoscedasticity conditions for parametric tests.

RESULTS

Ranges and relationships among grass measures

The means and ranges of measures taken on clipped samples from this study site are similar to those cited in studies at nearby locations (Table 1). Dry green biomass densities varied from 13 to 361 g/m^2 with a global mean of 102 g/m^2. These green biomass values echo those reported by McNaughton (1985) at sites just south of our study area. Protein densities ranged from 1 to 37 g/m^2. Protein density should equal the product of dry green biomass density and the fraction of the dry green moiety that is protein (called *fraction protein* subsequently). As can be seen in Fig. 3, most of the variation in protein density is due to variation in dry green biomass density (r^2 = 91.7%), leaving only a small amount of residual variation attributable to fraction protein. Dry green biomass density in turn equals the product of sward height (in centimetres) and dry green bulk density (in milligrams of dry green biomass per cubic centimetre of sward volume). As a consequence, protein density is positively correlated with both sward height and dry green bulk density; sward height and dry green bulk density tend to be inversely related (Fig. 3 and Table 2). In a multiple regression, 56% of the overall variation in protein density is attributable to variation in dry green bulk density and an additional 35.7% is associated with sward height differences. These relationships vary somewhat with season and sample site.

The remaining measures on the clipped grass samples covaried with sward height and bulk densities and with each other in expected ways (Table 2). These measures are the fraction of wet clipped sample masses that is green (*fraction green*), the fraction of wet green material that is water (*fraction water*), and the fraction of green dry matter that is protein (*fraction protein*). Swards with a high fraction of green material also had higher water contents, protein fractions, heights, and bulk densities. Swards with higher water contents tended to have higher protein levels and bulk densities, but were not necessarily taller. Fraction protein showed a strong positive correlation with bulk density, but only a slight correlation with height.

Seasonal variation

Rainfall, protein density, and gazelle density all covaried over time (Fig. 4). This covariation suggested

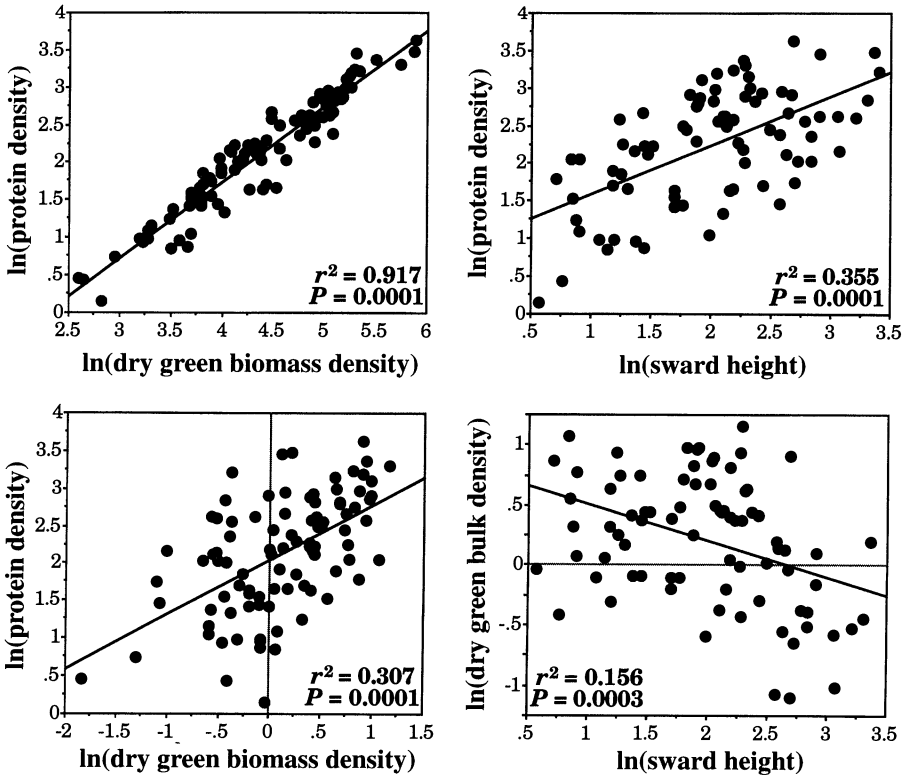

FIG. 3. Relationships among protein (g/m^2), dry green biomass density (g/m^2), dry green bulk density (mg/cm^3), and sward height (cm).

that some partitioning into seasons was justified. Even during the periods of heaviest rains, weekly rainfall at the site was erratic, and so a criterion based on weekly or daily rainfall alone was difficult to establish. In addition, the lags between changes in rainfall and corresponding responses by swards and gazelles suggested that changes in protein and gazelle densities might be better criteria for defining seasons. Setting 1 January 1990 as day 1, day −12 was the first day that both protein and gazelle densities moved consistently above their annual means, and day 172 was the first day both measures dropped and remained below annual means. In retrospect, these cut-offs fit the most reasonable criterion for rainy season onset based on rainfall alone, and lag the cessation of heavy rains by only a week. We thus assigned days −80 through −13 to the end of the first dry season, days −12 through 171 to the wet season, and days 172 through 225 to the beginning of the second dry season.

We then determined which sward parameters showed variation linked to season and/or sample area. Wet biomass densities and sward compositions varied with both season and sample site (Fig. 5). The first set of samples was taken at the end of a long dry season from throughout the global area; the second set of dry-season samples was taken from the central area after the end of the rainy period. The total wet biomass in the first dry-season sample was over twice that in the second. However, nearly 60% of the former sample was brown material, whereas only 41% of the second sample was brown. The second dry-season samples contained nearly twice as much water in the green moiety, but this was compensated by a 36% higher protein level. Despite these marked compositional differences, the resulting mean protein densities are not quite significantly different for the two samples: 6.5 ± 0.5 g/m^2 (mean ±1 SE) for the first dry season on the global site, and 4.3 ± 0.7 g/m^2 for the second dry period on the central site ($F_{1,50} = 3.16$, $P = 0.08$). The two wet-season samples followed each other in time: the first was taken in the global area and the second in the central area. Not surprisingly, given the longer period

TABLE 2. Correlation matrix for selected measures taken on sward clippings from throughout study sites and study periods. Parameters were transformed where necessary to ensure normality and homoscedasticity. All Pearson correlation coefficients marked with * are significant at $P < 0.05$ or smaller.

	Fraction green	Fraction water	Fraction protein	Sward height
Fraction water	0.652*			
Fraction protein	0.455*	0.592*		
Sward height	0.432*	0.115	−0.150	
Dry green bulk density	0.462*	0.675*	0.443*	−0.222*

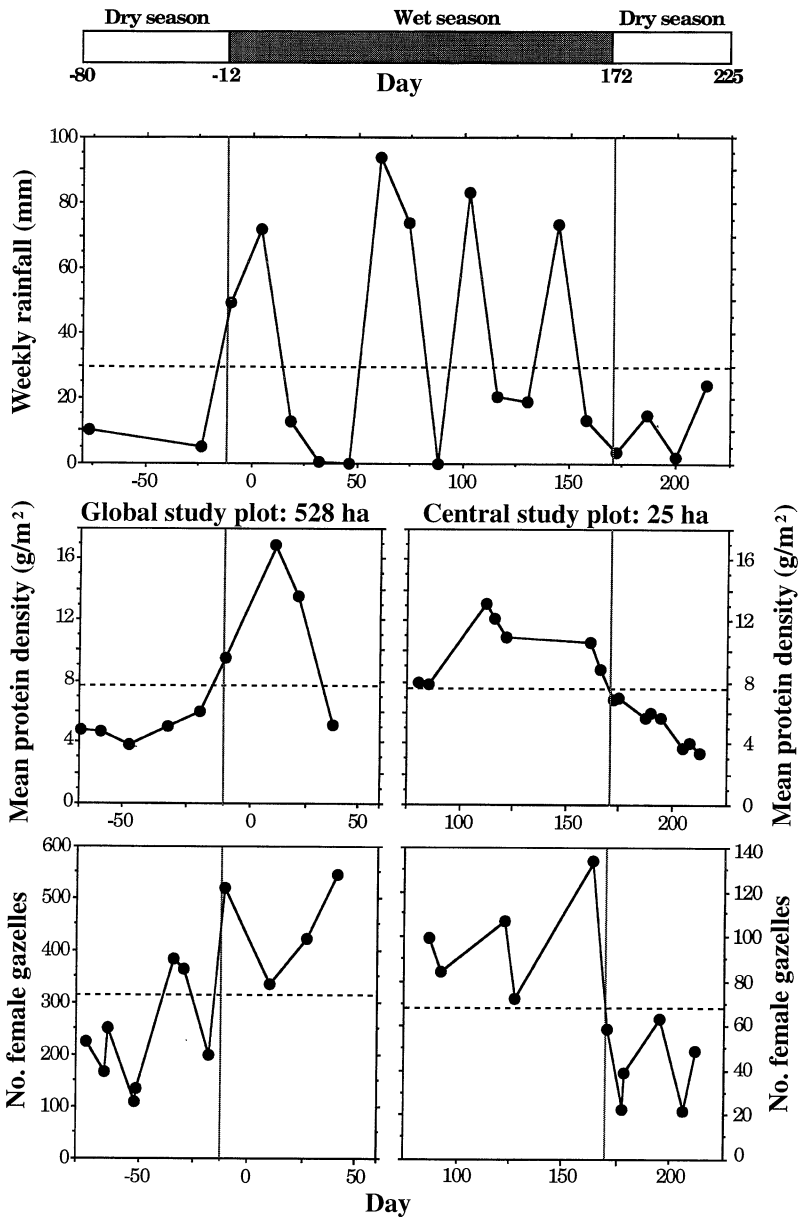

FIG. 4. Rainfall, protein density, and total number of female Thomson's gazelles on the study site as function of date. Dates are given as numbers of days before or after 31 December 1989. Protein densities and gazelle numbers are given for global sample area for dates between −75 and 70; values for later dates refer to the central sample area only. Partitioning of the study period into first dry season, wet season, and second dry season is shown at the top of the figure. Note the different scale for number of female gazelles for the two study plots.

of prior rainfall, the second wet-season sample shows much higher wet biomass densities than the first. Compositionally, the two wet-season samples show similarly low fractions of brown material: 12.3 and 13.5%, respectively. However, samples from the first half of the wet season had a lower water content than samples from the second half, 35.8 vs. 49.6%, whereas those from first half had higher protein levels than the second (5.5 vs. 4.2%). Again, the trade-offs between total biomass and composition give mean protein densities that are not quite significantly different for the two samples: 14.8 ± 2.0 g/m² for the first wet season sample on the global site, and 18.7 ± 1.4 g/m² for the second wet season sample on the central site ($F_{1,33} = 3.05$, $P = 0.09$). Because the clipped samples were not taken randomly, it is possible that the patterns of mean protein densities noted above were not representative. However, this can be checked by using the estimated protein densities from the green-machine scans, which provided uniform coverage throughout each study area. In the

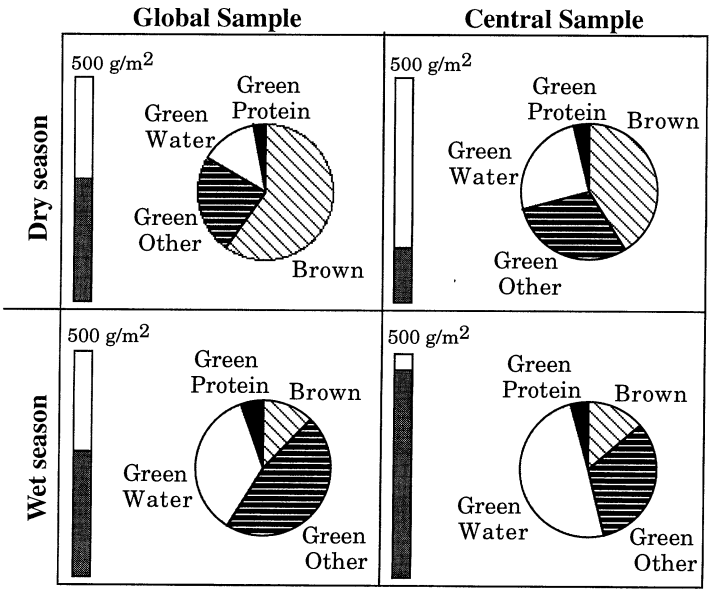

FIG. 5. Wet biomass densities and sward compositions from global area in first dry season (top left), global area in first half of subsequent wet season (lower left), central area during second half of wet season (lower right), and central area during second dry season (top right). The scale on the left of each figure shows mean wet biomass density relative to the site maximum of 500 g/m^2. The pie chart in each case shows the fraction of this wet biomass due to brown material, protein in the green moiety (green protein), dry matter in the green moiety other than protein (green other), and water in the green moiety (green water).

dry season, the global sample mean was 4.6 ± 0.4 g/m^2 and the central sample was 5.3 ± 0.5 g/m^2; the corresponding wet-season values were 11.3 ± 2.6 and 10.2 ± 0.8 g/m^2. A two-way ANOVA of these estimated protein values with season and sample site as factors showed a significant effect of season (wet vs. dry; $F_{1,21} = 30.7$, $P < 0.0001$), but no significant effects of either sample site (global vs. central) or the interaction between factors (both $F_{1,21} < 0.71$). Thus, although there are major differences in total biomass density and physiognomy between sample sites within a season, protein densities tend to be similar. Protein densities between seasons, however, do differ markedly: values in the wet season are consistently 2–3 times those in the dry season.

As noted earlier, sward measures such as fraction green, fraction water in the green moiety, fraction protein in the dry green portion, height, and bulk density of dry green material tend to covary between samples. To characterize physiognomic and compositional changes between seasons and sample sites, we reduced these five correlated parameters to a smaller number of uncorrelated variables using principal components analysis. The first two principal components explained 79.5% of the variance in the original matrix. The first component heavily weighted all of the parameters that contribute to sward compositional quality: fraction green, fraction water, fraction protein, and bulk density. The second component was dominated by fraction green and sward height. A plot of the factor scores for these two components is shown in Fig. 6 with different season and sample site data indicated by different symbols. This graph suggests that there are significant effects of both season and sample on factor values. A two-way ANOVA of the first component with season (wet vs. dry) and study area (global vs. central) as factors showed significant effects of season ($P = 0.031$), study area ($P = 0.003$), and their interaction ($P = 0.017$). The major effect here was the much higher values of fraction green and bulk density in the central area during the wet season when compared to the dry; equivalent means for the global study area were only slightly different between the two seasons. Similar analysis for the second component shows significant effects of season and the season–study area interaction (both $P < 0.0001$), but no significant effect of study area alone ($P = 0.095$). The seasonal effect reflects the higher swards during the wet season in both study areas. However, global study area samples during the wet season tend to be taller but lower in bulk density and compositional parameters than equivalent samples from the central area. Similarly, if the dry-season data are pooled across the two study area sites (as justified by the lack of a study area effect in the ANOVA), the negative correlation between the two principal components is significant ($r^2 = 0.167$, $P = 0.0026$), again reflecting the inverse relationship between height and bulk density measures noted previously.

A regression of the logarithm of protein density measured in clippings on the two principal components explained 64.5% of the variance in the dependent variable ($P < 0.0001$). The amount of variance explained by the first principal component ($r^2 = 0.326$, $P < 0.0001$) was very similar to that explained by the second ($r^2 = 0.319$, $P < 0.0001$). Dashed lines in Fig. 6 indicate isopleths of equal protein density estimated from this regression. The fact that the slopes of these lines are close to −1.0 reflects the nearly equal contributions of both principal components to overall protein levels.

The preceding analyses indicate how various sward parameters vary with season and site and how they

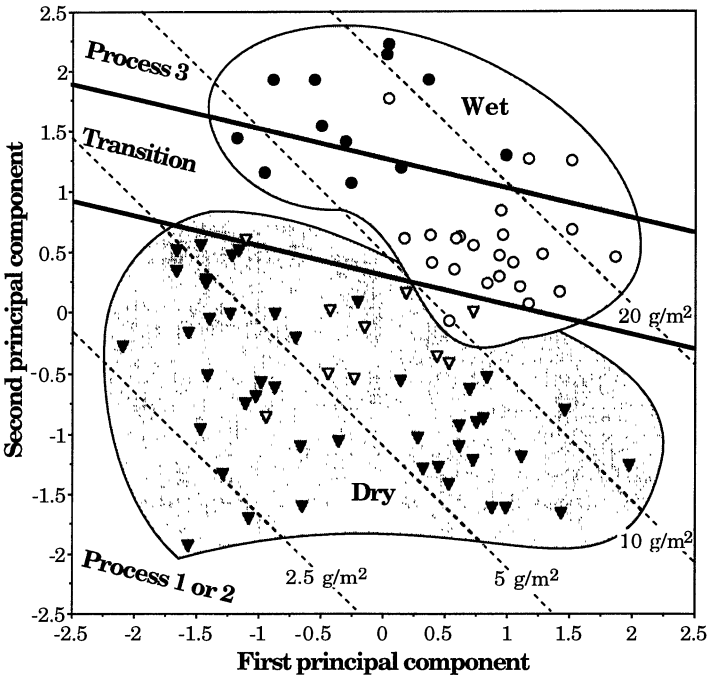

FIG. 6. Plot of first two principal component factor scores (varimax orthonormal solution) for five sward measures. The first component accounts for 53% of the variance and has the following loadings: fraction green 0.673, fraction water 0.877, fraction protein 0.789, sward height −0.137, and dry green bulk density 0.844. The second component accounts for an additional 27% of variance and has the following loadings: fraction green 0.629, fraction water 0.240, fraction protein −0.078, sward height 0.960, and dry green bulk density −0.150. Global area data are indicated by filled symbols, and central area data by open symbols. Wet-season samples are circles; dry-season samples are triangles. Dashed lines show isopleths of constant protein density. Dark lines are logistic regression cutoffs separating sward samples into those associated with Process 3 foraging (region above top dark line), with Process 1 or 2 foraging (region below lower dark line), or with the transition between Process 3 and Process 1 or 2 foraging (region between two dark lines).

contribute to protein density. The actual parameter measured in association with our behavioral data was not protein density but the surrogate, vegetation index. We thus need to know whether the variations with season and site in parameters determining protein density also affect vegetation index and if so, whether they do so in the same ways. An ANCOVA was undertaken with vegetation index as the dependent variable, season (wet vs. dry) and study area (global vs. central) as factors, and sward height, dry green bulk density, fraction green, fraction water, and fraction protein as covariates. Interaction terms between each of the covariates and season, and each covariate and study area site were also entered. The only significant covariates were height, dry green bulk density, and fraction protein (all $P < 0.0001$). These three covariates alone accounted for 59.1% of the observed variation in vegetation index. The factors season and study area were both significant ($P < 0.0001$ and $P = 0.014$, respectively), with the wet season and central study area each being associated with higher overall vegetation indices. Season explained another 11.4% and study area 2.3% of the remaining variation in vegetation index. There were no significant interactions. The relative dependence of vegetation index on sward height, bulk density, and fraction protein for each season and site combination is shown in Table 3. In the dry season on the global site, all three parameters contribute significantly and equally to vegetation indices. This is the only period and site at which protein density variation was significantly related to vegetation index. During the early wet season, as measured on the global site, the only significant correlate of vegetation index was height. On the central site in both seasons, height and bulk density both make significant contributions, with bulk density playing a slightly larger role. Clearly, vegetation index varies in ways that make it a reliable and representative measure of variations in protein density, and of the sensitivity of the latter to changes in sward height, bulk density, and fraction protein.

TABLE 3. Results of multiple regressions of vegetation index on sward height, bulk density, and fraction protein for each site and season combination. Values in table are r^2 for each independent variable or combination (all variables). Significance values marked with * have $P < 0.05$, and those marked with † have $P < 0.005$.

Variable	Global dry	Global wet	Central wet	Central dry
Height	0.241†	0.329*	0.153*	0.301*
Bulk density	0.240†	0.083	0.158*	0.488†
Fraction protein	0.241†	0.169	0.084	0.020
All variables	0.722†	0.572*	0.396*	0.809*

Gazelle bite rates in the dry season

A plot of bites/min foraging vs. underlying protein density for our entire data set shows a curvilinear relationship that does not follow the rising and asymptotic form expected for Type II functional responses (Fig. 7). Instead, bite rates rise as protein densities increase from 2 up to ≈12–13 g/m², and then decrease with increasingly higher protein densities. In addition, the variation in bite rates for lower protein densities is much higher than that for higher values. Both observations suggest that different processes are controlling bite rates at lower and higher protein densities. As sug-

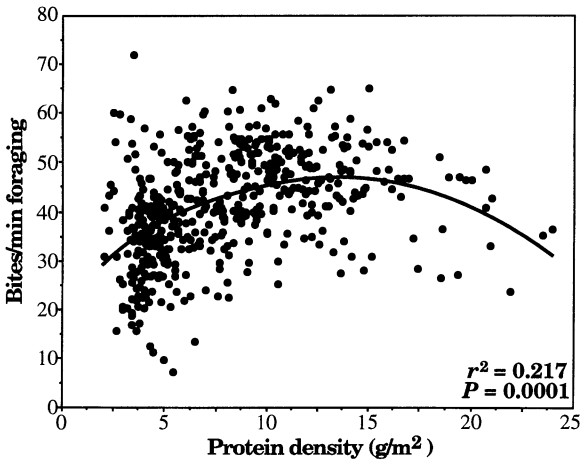

FIG. 7. Relationship between pooled wet- and dry-season bites/min foraging (number of bites recorded in a sample divided by number of minutes of foraging) and underlying protein densities. The curve for quadratic regression is shown: both the first- and second-order coefficients are significant at $P < 0.0001$.

gested by *Ranges and relationships among grass measures,* above, this heterogeneity in process could be due to the pooling of wet and dry seasons, to the pooling of global and central samples, or both.

We first subdivided the data according to season. A separate plot for dry-season within-bout bite-rate data (global and central data pooled) shows a pattern more like that of a Type II functional response (Fig. 8). Gross bite rate and bites/min foraging measures exhibit similar patterns. However measured, bite rates reflect a decelerating and asymptotic positive relationship with underlying protein densities. This pattern could be explained by either Process 1 or Process 2 of Spalinger and Hobbs (1992). These models assume foraging to be the only activity and thus gross bite rate, which includes time spent on nonforaging matters, might not be expected to fit either model as well as the other measures. Similarly, our within-bout bite measure, which excludes time spent on head-ups, might also be expected to be a poor fit to Process 1 if searching in the dry season is in part dependent upon head-ups. If dry-season search does not require head-ups, then the within-bout data could show a good fit to either model. We used nonlinear regressions to examine the fit of both Process 1 and Process 2 models to each of our three dry-season bite measures. Process 1 models were of the form

$$\text{bite rate} = \frac{V_{\max} Wk(\text{protein density})}{1 + hV_{\max} Wk(\text{protein density})}$$

where all bite rates are given as number of bites per minute (Spalinger and Hobbs 1992). $V_{\max}$ is the foraging velocity of a gazelle exclusive of time spent biting; as a gazelle stops to take more bites, its overall velocity will decrease below this value. Using allometric relations described by Pennycuik (1979), Illius and Fitzgibbon (1994) estimated the maximum walking speed of a Thomson's gazelle to be 44.29 m/min. The fastest velocity observed in a foraging female gazelle in our study was close to this limit at 42.9 m/min. We thus used the former value in our regressions. W is the width of the effective search path of a foraging gazelle. From videos of foraging Thomson's gazelles, we estimated this to be 0.84 m. Protein density is the mean estimated value underlying each foraging animal and is entered as g protein/m^2. The parameters h and k are estimated by the regression: h is the minimal time (in minutes) required to procure a bite once it is located and approached; the asymptotic bite rate predicted by this model at high protein densities is equal to the reciprocal of h. The parameter k is a constant of proportionality between protein density and the density of bites. Inclusion of k in this manner tacitly assumes that bite density and protein density are linearly related. Process 2 regressions were based upon the model

$$\text{bite rate} = \frac{V_{\max} \sqrt{k(\text{protein density})}}{1 + hV_{\max} \sqrt{k(\text{protein density})}}$$

where all terms and parameters are as for the Process 1 regressions (Spalinger and Hobbs 1992).

Both Process 1 and Process 2 models generated significant fits for all three dry-season bite rate data sets (all $P \leq 0.0002$). The fits were worst for the gross bite rate data ($r^2 = 0.070$ and 0.086 for Processes 1 and 2, respectively), better for bites/min foraging ($r^2 = 0.139$ and 0.155), and best for within-bout bite rates ($r^2 = 0.218$ and 0.237). Although fits were consistently better with the Process 2 model, the model differences were not significant in any case ($F_{229, 229} < 1.03$ for all measures). It is of interest that the within-bout bite rates give the best fits even for a Process 1 model: if search is a limiting factor for bite rates in the dry season, it apparently does not require head-ups.

Estimated asymptotic bite rates (using the reciprocals of the estimated h values) for gross, bites/min foraging, and within-bout conditions were 45.5, 50.8, and 60.6 bites/min, respectively, given a Process 1 model; equivalent values for Process 2 were 77.5, 82.6, and 98.0 bites/min. The maximal bite rate observed in the dry season was 66.8 bites/min and the maximal rate seen at any time in the study was 77.8 bites/min. Whereas these values fall within the 95% confidence limits of Process 2 estimations, they fall outside of those for the Process 1 model. However, standard errors for the Process 2 model are larger than those for Process 1.

Estimates of k (no. bites per gram of protein per square metre) for Process 1 models ranged from 0.67 to 0.87, whereas those for Process 2 fits ranged from 0.34 to 0.63. The different range for the Process 2 estimates is expected, given the scaling of the protein density by a square root in the latter case. Because $V_{\max}$, W, and k are always multiplied together where

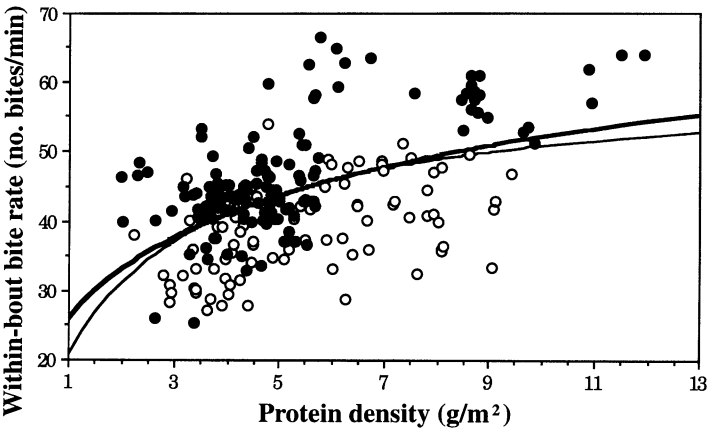

FIG. 8. Dry-season within-bout bite rates vs. protein density. Solid points indicate global area data; open points indicate central area data. The thin line indicates Process 1 model fit ($r^2 = 0.218$, $P < 0.0001$), and the dark line shows fit to the Process 2 model ($r^2 = 0.237$, $P < 0.0001$).

they appear in the Process 1 equation, they cannot be independently estimated by the regression; instead, their product is estimated. Similarly, in Process 2 regressions, a product of V_{max} and k is the estimated number. For this reason, estimates of k are inversely related to the presumed values of V_{max} and W. Whereas search width, W, seems unlikely to be much different from our estimate, the value of V_{max} used in the above regressions is the maximum walking velocity of a gazelle (Pennycuick 1979). It is possible that the optimum velocity exhibited between bites when the animal is searching for forage in a particular habitat is lower than the maximal walking velocity of 44.29 m/min (Gendron and Staddon 1983). One way to test this possibility is to use the fact that for both Process 1 and 2 models, the observed foraging velocity, V, is related to observed bite rate, B, as $V = V_{max} - hV_{max}B$. A linear regression of V on B should give an ordinate intercept equal to V_{max}. Using our measures of bite rates and velocity, we obtain estimates of V_{max} of 14–17 m/min, depending upon the bite rate measure and sample. These are much lower values than the 44.29 used in the previous nonlinear regressions. If one repeats the latter with a V_{max} of 15 m/min, the range of estimated k values rises to 1.98–2.55 for Process 1 fits, and 2.96–5.5 for Process 2 models. Estimates of h and r^2 values are unchanged by varying V_{max}. As we shall report in a subsequent paper (S. L. Vehrencamp, J. W. Bradbury, and K. E. Clifton, *unpublished manuscript*), there are other reasons to believe that actual values of V_{max} are less than the maximal walking velocity and in fact may vary both between and within seasons. This makes the higher values of k more likely. In the present context, however, this does not affect either the degree of fit of the regressions or the estimates of the maximal bite rates.

A close perusal of Fig. 8 suggests that dry-season bite rates in the global study area tend to be higher for a given protein density than those for the central study area. This is particularly evident for within-bout rates and higher protein densities. This impression is perhaps exaggerated by the fact that only the global study area had sites utilized by gazelles with protein densities >9.5 g/m^2. We thus examined regression models for each study area separately. Visual inspection indicated that all three measures of bite rate rise monotonically with protein density in both study areas. It is not surprising then to find that no dry-season sample from either site gives a significant fit to a Process 3 model. Fitting each study area separately to Process 1 and Process 2 models (and using $V_{max} = 44.29$ m/min for comparison with pooled analyses) produces highly significant fits for both models in every case. As with the pooled study area data, the unpooled study area regressions do not produce significantly better fits for either Process 1 or 2. However, parameter estimates are significantly different for the two study areas ($F_{2, 227} > 12.0$, $P < 0.001$ for each of the three bite measures and two processes). Using Process 1 models, estimated values of h are 30–40% lower for the global than those for the central study site; Process 2 values are an average 81% lower for the global area sample. This difference will cause the global area samples to have a higher asymptotic bite rate. In contrast, the estimates of k, the hypothesized proportionality constant between protein density and bite density, are 7–20% lower in the global area data than in those from the central site. This would cause the central area bite rates to rise a bit more rapidly to their asymptote as protein densities increased than did those from the global area. Because bite rates for the global area are consistently higher than those of the central area at every protein density and for all three bite measures, the smaller values of h from the global data clearly outweigh the smaller values of k.

To check the assumption that bite densities and protein densities could be modeled linearly, each bite-rate measure was compared to a Process 2 model in which an allometric relationship between bite density and protein density was incorporated explicitly (e.g., bite density = k(protein density)^g, where both k and g are constants). The prior regressions presumed the same equation but tacitly set $g = 1$; this new set allowed g to be any value. It was also assumed that the minimum time required per bite, h, was the reciprocal of the maximal

bite rate observed in any season (77.8 bites/min). When global and central samples were pooled, regressions gave exponents (g) of 0.917 (95% CL = 0.528, 1.310) for gross bite rates, 1.003 (CL = 0.696, 1.314) for bites/min foraging, and 1.205 (CL = 0.916, 1.499) for within-bout rates. Similar values but with much larger standard errors were obtained by fitting global and central data separately. We feel these estimates for g are all sufficiently close to 1.0 to justify the use of the linear approximation between bite density and protein density used in the first set of regressions. Estimates of the proportionality constant, k, were similar to those obtained in the earlier pooled regressions using a fixed value of V_{max}.

To conclude this section, it appears that our dry-season data from both global and central areas support either Process 1 or Process 2 foraging. This implies that bite density is the critical factor limiting bite rates during this period. Bite density, in turn, appears to be linearly related to protein density. Because the estimated time per bite, h, is lower for the global area data than for the central ones, bite rates at any given protein density appear to be higher in the former site.

Gazelle bite rates and bite masses in the wet season

The relationship between bite rates and underlying protein densities in the pooled wet seasons is negative and thus differs markedly from our dry-season samples (Fig. 9). Linear regressions of each bite-rate measure on protein density showed significant negative relationships although there was considerable scatter about the fitted lines (gross bite rate: $r^2 = 0.045$, $P < 0.0005$; bites/min foraging: $r^2 = 0.053$, $P < 0.0001$; within-bout bite rate: $r^2 = 0.019$, $P = 0.024$). This negative relationship is precisely what is expected when Spalinger and Hobbs' Process 3 is operative and the opposite of that expected for either Process 1 or 2. Because wet-season data extend to higher protein values than dry-season samples, the descending right-hand side of the unimodal curve in Fig. 7 can then be explained as the expected pattern, given that wet-season foraging follows Process 3 rules.

Because bite rates do not drop off rapidly over the range of protein densities observed in our wet-season samples, the actual shape of the function is difficult to discern. To test for a Process 3 fit specifically, we used nonlinear regression to fit the wet-season bite-rate data to the following model:

$$\text{bite rate} = \frac{R_{max}}{S + hR_{max}}$$

(Spalinger and Hobbs 1992). Here, R_{max} is the maximum rate at which a female gazelle can chew and swallow accumulated bites and is measured in grams of dry green biomass per minute. Using allometric relationships provided by Shipley et al. (1994), R_{max} for a 20-kg Thomson's gazelle should be 5.738 g/min. The value of h, the minimum time to make a bite, should equal the reciprocal of the maximal wet-season bite rate. As noted above, the highest bite rate we observed at any time in our study was a within-bout rate of 77.8 bites/min. This gives a value for h of 0.0129 min/bite. Subsequent reanalyses using both higher and lower maximal bite rates showed that the assumed value for h has little affect on the quality of the fits or on the estimated parameters. S is bite mass (in grams of dry green biomass per bite), and is an unknown quantity.

Bite mass can be modeled as a power function of underlying forage abundance. Such a model is of the form bite mass = g(forage density)^a, where the exponent a routinely is <1.0; our computations from published data on sheep and cattle give values of a between 0.15 and 0.5 (Hodgson 1985, Hudson and Watkins 1986, Forbes 1988, Burlison et al. 1991, Laca et al. 1992, 1994, Flores et al. 1993). Assuming the values for R_{max} and B_{max} cited above and an allometric relation between bite mass and underlying protein density, we can rewrite the Process 3 bite-rate equation for Thomson's gazelles as

$$\text{bite rate} = \frac{5.7375}{g(\text{protein density})^a + 0.0738}.$$

The appropriate bite-rate measure would seem to be bites/min foraging, since gross bite rate incorporates time spent on activities other than foraging, and within-bout rate might overestimate true values by deleting head-up time spent chewing and swallowing. However, we examined nonlinear regressions of observed bite rate vs. underlying protein density for all three measures. Fitted parameters were g and a. These parameters were then used to estimate bite masses from protein densities.

The results generated significant regressions for all three measures of bite rate, although the amount of variation explained is low and similar to that for the linear regressions. As expected the best fit was obtained with the bites/min foraging measure (gross bite rate: $r^2 = 0.031$, $P = 0.015$; bites/min foraging: $r^2 = 0.043$, $P = 0.0028$; within-bout rate: $r^2 = 0.028$, $P = 0.021$). Only the within-bout regression gives a better fit than a linear model, and none are significantly different from the linear models. The fitted parameter values for the bites/min foraging regression were $g = 0.0294$ (95% CL = 0.0218, 0.0393), and $a = 0.2185$ (CL = 0.0923, 0.3466). It is reassuring that the exponent a is in the same range as that found in published studies of other grazers. The two parameters were then used to estimate bite masses from underlying protein densities for each behavioral sample. The resulting computations gave bite mass values of 5.8–175 mg dry green biomass/bite. These values are similar to those estimated for Thomson's gazelles by Illius and Fitzgibbon (1994) using very different assumptions and data. We conclude that the negative relationship between bite rates and protein density in the wet season reflects Process 3 foraging rules during this period.

It is also possible to rewrite the Process 3 equation so that bite mass is a function of bite rate and the constants R_{max} and B_{max}. Bite masses can then be estimated for each focal sample using observed bite rates as long as Process 3 conditions are assumed to apply. The preferred measure is again bites/min foraging. Fitting estimated bite masses (in grams of dry green biomass/bite) to the nonlinear allometric model,

$$\text{bite mass} = g(\text{protein density})^a$$

should give a fit and parameter values similar to those obtained with the method used above. The fit of this second model using bites/min foraging had an $r^2 = 0.042$ ($P = 0.003$), and values of $g = 0.0287$ (95% CL = 0.0192, 0.04145) and $a = 0.2655$ (CL = 0.1089, 0.4303). Results using the two possible estimation sequences are thus very similar quantitatively and both support the conclusion that bite mass for the wet season rises with increasing protein density in a monotonic but decelerating way (e.g., $0 < a < 1$).

If there were an asymptotic bite mass (either because of spatial properties of the sward, or because of the fixed dimensions of the gazelle's teeth), then a nonlinear regression using an asymptotic model might give a better fit of bite mass vs. protein density. In fact, asymptotic regressions give a slightly worse fit than the allometric models ($r^2 = 0.027$, $P = 0.025$), but the differences between the asymptotic and allometric fits are not significant ($F_{264,264} = 1.01$). For what it is worth, the asymptotic bite mass estimated by this third approach was 67 mg of dry green biomass/bite.

It is again important to ask whether there are significant differences between the fits of the global and central wet-season samples to alternative foraging models. None of the measures from either global or central wet-season samples treated separately show significant fits to either a Process 1 or Process 2 model. All three global area wet-season bite measures give significant fits to a Process 3 model, and these fits are better than those obtained when global and central data are pooled (global area gross bite rates: $r^2 = 0.073$, $P < 0.05$; bites/min foraging: $r^2 = 0.172$, $P < 0.0001$; within-bout bite rates: $r^2 = 0.184$, $P < 0.0001$). Estimates of the allometric exponent a for the global samples alone were 0.350 (95% CL = 0.108, 0.601) for gross bite rates, 0.400 (CL = 0.228, 0.578) for bites/min foraging, and 0.389 (CL = 0.227, 0.559) for within-bout bite rates. The estimates of a are higher than when pooled with the central samples, but are still within the range seen in other grazers. Were we to use these parameters instead of those from the pooled values, estimated mean bite masses would be the same but those over the lowest protein densities would be ≈22% lower and those over the highest protein densities about ≈17% higher than values estimated using the pooled data parameters.

In contrast to global area data, central area wet-season bite rates show no significant relationships with underlying protein densities. This is true whether one tries to fit a linear regression, a Process 3 model ($r^2 < 0.01$ and $P > 0.3$ for each measure and model), or Process 1 or 2 models. A Process 2 model in which the value of h was permitted to increase linearly with protein density gave the best fit, but was still not significant (r^2 for bites/min foraging = 0.027, $F = 1.47$, $P > 0.20$). In summary, bite rates remain approximately constant with underlying protein densities in the central wet-season samples.

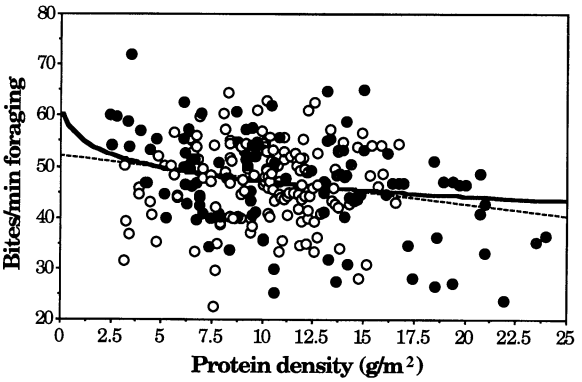

FIG. 9. Wet-season bites/min foraging vs. protein densities. Solid points indicate global area data; open points indicate central area data. The solid line is the Process 3 model fit ($r^2 = 0.043$, $P < 0.0028$), and the dashed line a linear model fit ($r^2 = 0.053$, $P < 0.0001$).

Gazelle bite rates and underlying forage parameters

The different types of relationships between bite rate and protein density in the four season–site combinations are most easily seen when bite rate is plotted against the logarithm of protein density (Fig. 10). This straightens out the regression lines and makes their slopes more evident. For each site, a Process 2 regression line is shown for the dry-season data, and a Process 3 line for the wet-season points. Process 1 lines could easily be substituted here for the Process 2 plots without changing the following arguments, and a Process 2 fit applied to the central area wet-season plot would have given a line with a slope similar to that of the Process 3 line shown. Equivalent plots for gross rates and bites/min foraging lead to identical conclusions and thus are not shown here.

Regardless of bite measure or study area, the dry-season samples show positively sloped relationships between bite rate and protein density with all of the global area regression lines having higher elevations than the corresponding central area ones. Wet-season samples show either flat (central area) or decreasing (global area) regression line slopes, and there are no differences between global and central area wet-season data in the elevations of the regression line midpoints.

These regression lines suggest a sequence of rising slopes (dry-season data from both study areas), flat slopes (wet-season central area), and finally descending

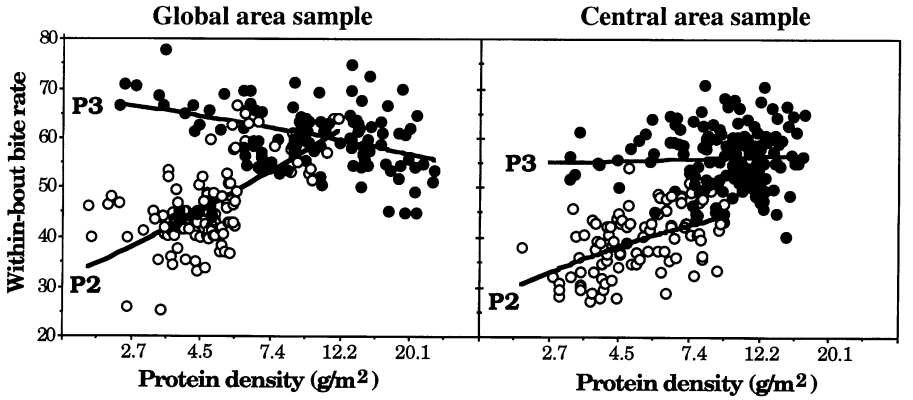

FIG. 10. Results of fitting models to global and central area and wet- and dry-season combinations separately. Dark circles are wet-season data, and open circles are dry-season data. P2 and P3 indicate Process 2 and Process 3 regression lines, respectively. Note that the protein x-axis uses a logarithmic scale, which straightens out nonlinear relationships.

slopes (wet-season global area). Thus the flat slope of the central area wet season appears to be a transitional phase between the positive slopes of the dry seasons and the negative slope of the global wet-season data. We assumed that this was the case and assigned one of the three slope types to each of our sward clipping samples according to where and when the sample was collected. We then performed an ordinal logistic regression of slope type on the two principal component scores derived for the clipping samples plotted in Fig. 6. The resulting regression explained 78.1% of the variation in slope types assigned to the clippings ($\chi^2 = 128.28$, $P < 0.0001$) and all intercept and coefficient values estimated by the regression were significant at $P < 0.003$ or less. It is instructive to superimpose these logistic regression cutoff lines separating slope types over a plot of the two principal component scores for the clipping data (Fig. 6). All sward samples with combinations of first and second principal component scores above the top cutoff line should be situations in which gazelles foraging on that sward have a negative slope type and thus follow Process 3 rules. All samples with principal component scores that plot below the lower cutoff line should show Process 1 or 2 foraging. Those swards with scores between the two lines should show the transitional state with a flat bite rate vs. protein density relationship. As can be seen, 91% of the assignments are correctly predicted by these cutoff lines.

As explained in an earlier section, Fig. 6 also shows isopleths of constant protein density. The fact that the slopes of these isopleths (all with slopes of -1.02) are steeper than those of the foraging process cutoff lines (slopes of -0.24) explains some puzzling outcomes of our earlier analyses. For example, bite-rate data taken over swards with identical protein densities show Process 1 or 2 during one season–study area combination, transitional relations in another, and Process 3 foraging in a third. Because of the different slopes for process cutoffs and protein density isopleths, it is now easy to see how this can occur (e.g., follow the 10 g/m^2 isopleth across the graph). In addition, the gentle slopes of the process cutoff lines suggest that it is the second principal component, strongly related to sward height, and not the first (which is related to compositional quality and bulk density measures), that determines which foraging process is experienced by the gazelles. Were both components contributing equally to control of foraging processes, we would expect the cutoff lines to have slopes of -1.0. If the first principal component were the dominant determinant of foraging process, the lines would be nearly vertical, and if the second component were the only determinant, they would be completely flat. The slight slope that we observe reflects the fact that the second principal component accounts for $\approx$81% of the determination of foraging process, whereas the first component accounts for only $\approx$19%.

There is another way to show the relationships between foraging process and underlying sward parameters. We performed linear regressions of bite rates on the logarithm of protein density for each of the global dry, global wet, central wet, and central dry samples. The slopes of these analyses were similar to those shown in Fig. 10, but were based on linear instead of nonlinear regressions. For each bite-rate measure, we regressed the slopes for the four samples on corresponding sward measures using bivariate regressions. The sward measures examined were the mean first and second principal components, sward height, and sward bulk density. Although there were only four points, significant regressions were obtained when these extracted slopes were regressed on the second principal component ($r^2 > 0.97$ and $P < 0.01$ for all three bite measures) and on height (all $r^2 > 0.92$ and $P < 0.04$), but not for regressions involving the first principal component (all $r^2 < 0.12$ and $P > 0.6$) or bulk density (all $r^2 < 0.02$ and $P > 0.85$). Although based on only a few points, these results confirm the role of sward height in controlling foraging process: as sward height increases, the slope of the linearized relationship be-

tween bite rate and protein density rotates continuously from ascending to flat to descending. Such a cycle was clearly evident in the global wet, central wet, and central dry sample sequence. Our failure to detect a flat period between the global dry season and the global wet is likely due to the extremely rapid growth of the swards that occurred once the rains began.

Estimates of gazelle intake

We estimated wet-season protein intake rates by multiplying each bite-rate measure by the corresponding estimate of bite mass (using parameter estimates from the pooled global and central wet-season data). These were converted into protein intakes by multiplying estimated dry green bite masses (in grams) by the average dry mass fraction of protein for the wet season (0.111) and by 1000 to convert the grams of protein into milligrams. The results of this computation for within-bout rates are shown in Fig. 11.

Process 3 intake rates (in milligrams of protein per minute) should be both decelerating and asymptotic in a manner similar to that seen for classical Type II functional responses. Given our conclusion that the pooled wet-season data best fit a Process 3 model, we thus used nonlinear regressions of the form

$$\text{intake rate} = \frac{a(\text{protein density})}{1 + [ha(\text{protein density})]}$$

to estimate the two parameters h and a. The reciprocal of h is equal to the asymptote in such a model, whereas the product ha determines how sharply the curve rises to the asymptote. The resulting regression line is superimposed on the individual estimate values in Fig. 11. The estimated maximal gross rate of intake in the wet season is 265.5 mg protein/min (95% CL = 244.4, 291.4); this regression explained 6.5% of the variation in gross intakes ($P < 0.0002$). The corresponding maximum for intake/min foraging was 294.3 mg protein/min (95% CL = 278.0, 313.1) and yielded an $r^2 = 0.124$ ($P < 0.0001$). The within-bout intake asymptote was 369.8 mg protein/min (CL = 354.6, 386.2) and the $r^2 = 0.276$ ($P < 0.0001$).

There was, unfortunately, no way to estimate bite masses from bite rates in the dry season because there is no trade-off between bite mass and bite rate in Processes 1 and 2. This made derived estimation of dry-season intakes impossible. It remains likely that bite mass in the dry season also follows a power function of underlying forage density with an exponent in the range 0.15–0.5. If we assume this to be true, one could at least provide a "scaled estimate" of dry-season bite mass by using any reasonable coefficient and exponent. As long as statistical contrasts are only made within a season and study area, this scaling would not affect conclusions. It does, however, assume that bite mass is monotonically related to underlying protein density in the same way for all points to be compared.

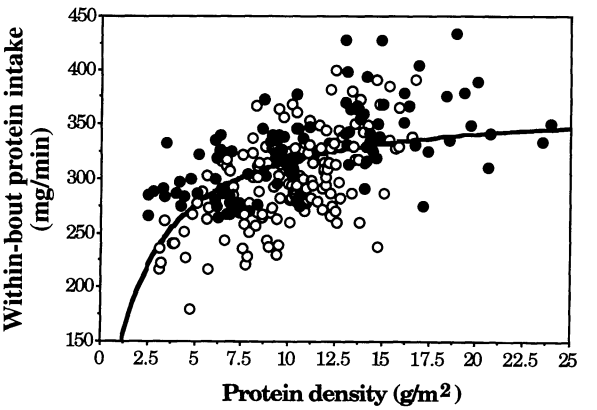

FIG. 11. Estimated wet-season within-bout intake rates. Dark circles are global area data; open circles are central area data. The regression line is the classical disc equation fit ($r^2 = 0.276$, $P < 0.0001$).

DISCUSSION

The seasonal changes in sward physiognomy at our study sites turn out to be quite important for interpretations of bite rates and intake patterns. The global dry data were collected in the last half of a dry season. Swards had an average wet biomass of 273 g/m^2, wide ranges in height, bulk density, and protein density, and nearly 60% of the wet biomass was brown (dead) material. As the rains began, brown material rapidly disappeared and was replaced by large amounts of tall green grass at low bulk densities. The average wet biomass remained nearly the same at 281 g/m^2, but protein densities increased to 2–3 times the dry-season values. The second half of the wet season was sampled in the central site. During this period and on this site, wet biomasses increased by 67% over the dry and wet global sample values, and heights were halved but bulk densities doubled. Because height and bulk density tend to be inversely related and their product explains the major fraction of the variation in protein densities, these changes in heights and bulk densities between the global and central wet-season samples were largely complementary, keeping protein densities at the same high level throughout the wet season. The final sample was the first half of the subsequent dry season measured on the central site. When compared to the global area dry-season samples, this period exhibited about half the wet biomass density and similar mean heights but considerably lower bulk densities (with much lower ranges of variation than seen on the larger site), about two-thirds as much brown material, and slightly lower protein densities. Some of the differences noted here are clearly related to seasonal changes, whereas others may be due to the fact that the central site was smaller and more homogeneous than the global area.

These large variations in sward characteristics ought to be reflected in concomitant changes in gazelle foraging behavior if the herbivore intake models of Spal-

inger and Hobbs (1992) are correct. Our results show fits among specific Spalinger and Hobbs models in each season–site combination: dry-season data from both the global and central sampling sites fit both Process 1 and Process 2 models; neither fits a Process 3 model. Wet-season data from the global site show a good fit to Process 3, but not to Process 1 or 2 models, and although the central wet-season data fit none of the models significantly, they appear to be transitional between Process 3 of the prior period and Process 1 or 2 of the succeeding one.

Nonlinear regressions using Spalinger and Hobbs models showed significant r^2 values ranging from 2.8 to 23.7% depending upon the bite rate measure examined and the season–study area site combination. Although these values may seem low, it must be remembered that no corrections have been made here for reductions in bite rate due to contextual factors other than underlying protein density. As we shall show in subsequent papers, bite rates are significantly affected by herd size, presence of adult males and infants, proximity to ruminating individuals, abundances of other ungulates, predator densities, and other extrinsic factors. But as we shall also show, these effects are additive and do not replace the direct effects of protein density on bite rate. One possibility is that critical cover used by gazelle predators is sufficiently linked to protein densities that it is increased predator risk, and not higher protein densities, that modulates bite rates. In fact, this argument cannot work for our study site as sward heights were so low even in wet seasons that predator cover was always nonexistent. It thus remains impressive that such strong and consistent fits to Spalinger and Hobbs' models are seen in our results despite the many other sources of bite-rate modulation. In both dry-season data sets, within-bout bite rates gave the strongest fits to the models. This was not true of the wet-season data when both global and central area samples were pooled, but was the case for the global area sample when it was examined individually. Within-bout rates exclude many of the extraneous activities that complicate the gross and bites/min foraging measures and thus might be expected a priori to show a tighter link with underlying resource levels. This was in fact what was found.

The model fits allowed us to estimate the relationships between protein density and bite density (which constrains Process 1 and 2 models) and bite mass (which constrains Process 3 foraging). In the dry seasons, bite density appeared to be isometrically related to protein density: for each gram of protein added to a square metre of sward, a fixed number of acceptable gazelle bites was added to that square metre. Our estimates of this proportionality constant depend upon the assumed value of maximal foraging velocity and whether Process 1 or Process 2 rules are invoked. If the maximal walking velocity of 44.29 m/min is used, constant estimates range from 0.27 to 0.87 bites·g protein^{-1}·m^{-2} depending on bite rate measure, study area, and presumed process. If a 15 m/min maximal foraging velocity (extrapolated from the observed relationship between foraging velocities and bite rates) is used, then the constant estimates range from 2.4 to 4.2 bites·g protein^{-1}·m^{-2}. In the wet season, bite mass was allometrically related to protein density with an exponent of $\approx$0.22 if global and central data are pooled, or of 0.40 if only the global area sample is considered. Allometric exponents between bite mass and underlying measures of biomass density in temperate grazers are usually $<$1.0 and tend to fall in the range 0.15–0.50 (Hodgson 1985, Hudson and Watkins 1986, Forbes 1988, Burlison et al. 1991, Laca et al. 1992, 1994, Flores et al. 1993).

Our analyses do not exhibit significant differences of fit for Process 1 and 2 models when applied to the same dry-season data. Process 2 models show slightly better fits than do Process 1 models, and the extrapolated asymptotic bite rates from Process 2 models are slightly closer to observed maxima than are those from Process 1 models. In addition, Spalinger and Hobbs predict that Process 1 foraging should shift to Process 2 rules when bite density is higher than the square of the reciprocal of search width (which was estimated from videos of foraging gazelles to be 0.84 m). The critical bite density would then be 1.42 bites/m^2. As noted above, the value of the proportionality constant between protein density and bite density varied inversely with the assumed value of maximal foraging velocity, V_{max}. However, even for the largest reasonable value of this velocity, we estimate nearly all bite densities in the dry season to be $>$1.42 bites/m^2. Although all of these observations suggest Process 2 over Process 1, it remains that we cannot provide a convincing case for one over the other. In terms of the general outcome, that bite rates are positively correlated in a decelerating way with protein densities in both dry seasons, it is not critical which of these two processes is operating.

Although global and central dry season data showed similar fits to a particular model (e.g., Process 1 or 2), the parameter estimates were different. Global samples showed a 30–80% shorter time per bite (h), and a 7–20% smaller value of proportionality constant between bite density and protein density (k), than was seen in the central area data. Decreases in the value of h raise the asymptote of the fitted nonlinear curve, whereas decreases in k lower the rate of rise to the asymptote. The difference between the two study areas in h values is much larger than that in k estimates. This explains the fact that for the same underlying protein density, bite rates from the global area are always higher than those from the central site.

Our data suggest that foraging in female gazelles follows a cycle of Process 3 foraging during wet seasons followed by Process 1 or 2 in dry seasons; there also may be transitional stages between the cycle phases. Which properties of the underlying swards appear to be driving these cycles? The answer cannot be

protein density per se: as we have seen, there are many instances in which gazelles foraging in a given season or site exhibit a process different from that seen in another season or site but over exactly the same protein density. It follows that only some of the components of protein density, or some unequal weighting of these components, drives the shifts among processes. Fig. 6 suggests that of the two principal components extracted from jointly measured fraction green, fraction water, fraction protein, sward height, and bulk density, it is the second component (which consists primarily of sward height and fraction green) that is most influential in determining foraging process: the higher this component, the more likely the gazelle is to be using Process 3 instead of Process 1 or 2. Increases in the first component (which weights all measures except height) can lower the minimal value of the second component required to trigger Process 3, but it takes a large change to do so. The results indicate that ≈81% of the determination of foraging process can be ascribed to the second component and only 19% to the first component. Gradual changes in the second principal component over time, particularly those due to changes in sward height, appear to control the slope of the linearized relationship between bite rate and underlying protein density in a continuous fashion: positive slopes at low sward heights become flattened as sward height increases (often with a concomitant drop in bulk density), and at high enough sward heights, the slopes rotate enough to become negative (e.g., bite rates decrease with increasing protein densities).

Within a season or site, the two principal components tend to be inversely related. Where the slope of this phenomenological relationship between the second and first principal components is gentle, it is easy to see in Fig. 6 that a wide range of protein densities may be present within that season and site without leading to any change in foraging process. In our data, this appears true of the global dry samples, which show a very large range of protein densities but no evidence of Process 3 succeeding Process 1 or 2. The slope of a linear regression between second and first principal components in this site and season (−0.35) is slightly steeper than that of the process cutoffs (−0.24), but much shallower than that of the protein isopleths (−1.02). Thus it crosses many protein isopleths but does not contact the nearest cutoff line within the ranges of the observed swards. This explains the wide range of protein densities with no change in foraging process. Readers should remember, however, that these cutoffs are based on only a single annual cycle and exact values might differ in subsequent years due to correlated factors that we may have failed to measure.

Spalinger and Hobbs (1992) predict that herbivores should shift from Process 2 to Process 3 foraging when the product of bite mass and the square root of bite density is greater than the ratio of maximum processing rate, R_{max}, to maximal foraging velocity, V_{max}. Do both bite mass and bite density have to increase to trigger a shift to Process 3, or does an increase in one component sufficiently dominate any decreases in the other? If the latter is true, which component dominates this switch, and how do sward parameters such as height and bulk density affect bite mass and bite density, respectively? We feel that the most likely chain of causation for our samples begins with a positive correlation between bite mass and sward height, and ends with a subsequent positive link between bite mass and the switch between Process 2 and Process 3 foraging. There are two arguments in favor of this sequence. First, the threshold condition at which Process 2 yields to Process 3 depends on the first power of bite mass but the square root of bite density. It thus takes a much larger increase in bite density to trigger this change than would be the case if bite mass were increased. A priori, this makes increasing bite mass a more likely cause of the shift to Process 3 foraging than increasing bite densities. Because we have found that increasing sward height is more important than increasing bulk density in promoting the shift between Process 2 and 3 foraging, it seems logical to conclude that bite mass is positively linked to height and either negatively or insignificantly related to bulk density.

The second reason arises from review of published studies on bite mass and density and underlying sward parameters on cultivated swards. A wide variety of previous studies have shown that domestic grazer bite masses increase with underlying biomass densities and that both sward height and sward bulk density contribute positively to this relationship (Hodgson 1985, Forbes 1988, Burlison et al. 1991, Penning et al. 1991, Ungar et al. 1991, Laca et al. 1992, Black and Kenney 1994). In most of these studies, sward height explains considerably more of the variation in bite mass than does bulk density (but see Stobbs 1973). As a consequence, bite masses on tall sparse swards are often greater than those on shorter but denser swards with the same biomass density (Black and Kenney 1984, Laca et al. 1992). A somewhat different pattern arises for bite density. In studies using continuous or very finely patched swards, one expects bite density to be proportional to the reciprocal of bite area. When cattle and sheep graze such swards, bite area tends to increase with sward height, but decrease with sward bulk density (Burlison et al. 1991, Laca et al. 1992); this causes bite density to be positively correlated with bulk density but negatively correlated with height. Tall, sparse swards would thus exhibit lower bite densities than would short, dense swards. If these general patterns also apply to our system, then the tall, sparse swards of the global wet season would be ones with high bite masses and low bite densities, whereas those from the central area wet- and dry-season samples would have lower bite masses but higher bite densities. In our study, it is the former in which Process 3 foraging is seen, and the latter in which Process 2 or transitional

foraging occurs. This supports the notion that sward height, acting through bite mass, dominates the determination of which foraging process is exhibited.

ACKNOWLEDGMENTS

We thank the Office of the President of Kenya for permission to undertake this study, and to Dr. David Andere, who served as our sponsor. This study would not have been possible without the unflagging encouragement and support of Dr. David Western. Dr. David Mwangi and his staff at the University of Nairobi provided advice, logistics, and distilled water at critical times. Our thanks to Mike and Judy Rainey and the Koiyaki Group Ranch Maasai for making it possible for us to work in this site and for support at all stages. Wild Heerbrugg in Switzerland kindly provided a rangefinder for this project and Etak Incorporated modified their navigator programs so that they would function properly near to the equator. Forrest Gompf developed the circuitry to monitor the rangefinder and tripod settings. Shirley Strum, Montague Demment, Robert Seyfarth, Dorothy Cheney, Joyce Pool, Cynthia Moss, Richard Leakey, and Holly Dublin all provided support and/or advice at various stages in the project. Serah Sailyalel, Benard Nzuma, Paulo Yikayo Ole Parmuaat, and Kennedy Maragore Ole Lepore each contributed to the data collection in the field, and Kim Karish, Deborah Hargrove, and Betsy van Holle helped analyze the massive amounts of data at the University of California at San Diego. Two anonymous reviewers contributed a number of important and helpful suggestions to improve the manuscript. The pilot work for this study was supported by a grant from the National Geographic Society (1985), and the subsequent funding was provided by NSF grant BSR-8717668.

LITERATURE CITED

Belovsky, G. E. 1984. Herbivore optimal foraging: a comparative test of three models. American Naturalist **124**:97–115.

Black, J. L., and P. A. Kenney. 1984. Factors affecting diet selection by sheep. II. Height and density of pastures. Australian Journal of Agricultural Research **35**:565–578.

Burlison, A. J., J. Hodgson, and A. W. Illius. 1991. Sward canopy structure and the bite dimensions and bite weight of grazing sheep. Grass and Forage Science **46**:29–38.

Clifton, K. E., J. W. Bradbury, and S. L. Vehrencamp. 1994. The fine-scale mapping of grassland protein densities. Grass and Forage Science **49**:1–8.

Clifton, K. E., and L. M. Clifton. 1991. A field method for the determination of total nitrogen in plant tissue. Communications in Soil Science and Plant Analysis **22**:851–860.

Demment, M. W., and G. B. Greenwood. 1988. Forage ingestion: effects of sward characteristics and body size. Journal of Animal Science **66**:2380–2392.

Flores, E. R., E. A. Laca, T. C. Griggs, and M. W. Demment. 1993. Sward height and vertical morphological differentiation determine cattle bite dimensions. Agronomy Journal **85**:527–532.

Forbes, T. D. A. 1988. Researching the plant–animal interface: the investigation of ingestive behavior in grazing animals. Journal of Animal Science **66**:2369–2379.

Gendron, R. P., and J. E. R. Staddon. 1983. Searching for cryptic prey: the effect of search rate. American Naturalist **121**:172–186.

Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. Ecology **74**:778–791.

Hassell, M. P. 1981. Arthropod predator–prey systems. Pages 105–131 *in* R. M. May, editor. Theoretical ecology: principles and applications. Sinauer, Sunderland, Massachusetts, USA.

Hodgson, J. 1985. The control of intake in the grazing ruminant. Proceedings of the Nutrition Society **44**:339–398.

Hudson, R. J., and W. G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. Canadian Journal of Zoology **64**:1705–1708.

Illius, A. W., D. A. Clark, and J. Hodgson. 1992. Discrimination and patch choice by sheep grazing grass–clover swards. Journal of Animal Ecology **61**:183–194.

Illius, A. W., and C. Fitzgibbon. 1994. Costs of vigilance in foraging ungulates. Animal Behaviour **47**:481–484.

Illius, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology **56**: 989–999.

Illius, A. W., and I. J. Gordon. 1991. Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. Journal of Agricultural Science **116**:145–157.

Illius, A. W., and I. J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia **89**:428–434.

Jiang, Z., and R. J. Hudson. 1993. Optimal grazing of wapiti (*Cervus elaphus*) on grassland: patch and feeding station departure rules. Evolutionary Ecology **7**:488–498.

Krebs, J. R., and N. B. Davies. 1987. An introduction to behavioral ecology. Sinauer, Sunderland, Massachusetts, USA.

Laca, E. A., R. A. Distel, T. C. Griggs, and M. W. Demment. 1994. Effects of canopy structure on patch depression by grazers. Ecology **75**:706–716.

Laca, E. A., E. D. Ungar, N. Seligman, and M. W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science **47**:91–102.

Lundberg, P., and M. Åström. 1990. Functional response of optimally foraging herbivores. Journal of Theoretical Biology **144**:367–377.

McLain, D. H. 1974. Drawing contours from arbitrary data points. Computer Journal **17**:318–324.

McNaughton, S. J. 1979. Grassland–herbivore dynamics. Pages 46–81 *in* A.R.E Sinclair and M. Norton-Griffiths, editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

———. 1985. Ecology of a grazing system: the Serengeti. Ecological Monographs **55**:259–294.

Motulsky, H. J., and L. A. Ransnas. 1987. Fitting curves to data using nonlinear regression: a practical and nonmathematical review. FASEB Journal **1**:365–374.

Owen-Smith, N. 1993. Evaluating optimal diet models for an African browsing ruminant, the kudu: how constraining are the assumed constraints? Evolutionary Ecology **7**:499–524.

Pearson, R. L., L. D. Miller, and C. J. Tucker. 1976. Handheld spectral radiometer to estimate graminaceous biomass. Applied Optics **15**:416–418.

Penning, P. D. 1986. Some effects of sward composition on grazing behaviour and intake by sheep. Pages 219–226 *in* O. Gudmundsson, editor. Grazing research at northern latitudes. Plenum, New York, New York, USA.

Penning, P. D., A. J. Parsons, R. J. Orr, and T. T. Treacher. 1991. Intake and behaviour responses by sheep to changes in sward characteristics under continuous stocking. Grass and Forage Science **46**:15–28.

Penning, P. D., G. L. Steel, and R. H. Johnson. 1984. Further development and use of an automatic recording system in sheep grazing studies. Grass and Forage Science **39**:345–351.

Pennycuick, C. J. 1979. Energy costs of locomotion and the concept of "foraging radius." Pages 164–184 *in* A. R. E.

Sinclair and M. Norton-Griffiths, editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Shipley, L. A., J. E. Gross, D. E. Spalinger, N. T. Hobbs, and B. A. Wunder. 1994. The scaling of intake rate in mammalian herbivores: the allometry of food intake in heterogeneous environments. American Naturalist **143**:1055–1082.

Shipley, L. A., and D. E. Spalinger. 1992. Mechanics of browsing in dense food patches: effects of plant and animal morphology on intake rate. Canadian Journal of Zoology **70**:1743–1752.

Spalinger, D. E., T. A. Hanley, and C. T. Robbins. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. Ecology **69**:1166–1175.

Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist **140**:325–348.

Stobbs, T. H. 1973. The effects of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. Australian Journal of Agricultural Research **24**:809–819.

Ungar, E. D., A. Genizi, and M. W. Demment. 1991. Bite dimensions and herbage intake by cattle grazing short, hand-constructed swards. Agronomy Journal **83**:973–978.

Ungar, E. D., and I. Noy-Meir. 1988. Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. Journal of Applied Ecology **18**:63–82.

Vivås, H. J., and B.-E. Saether. 1987. Interactions between a generalist herbivore, the moose, *Alces alces,* and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. Journal of Animal Ecology **56**:509–520.

Vivås, H. J., B.-E. Saether, and R. Andersen. 1991. Optimal twig-size selection of a generalist herbivore, the moose *Alces alces*: implications for plant herbivore interactions. Journal of Animal Ecology **60**:395–408.