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Exploring behavior of an unusual megaherbivore: a spatially explicit foraging model of the hippopotamus

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Abstract

Herbivore foraging theories have been developed for and tested on herbivores across a range of sizes. Due to logistical constraints, however, little research has focused on foraging behavior of megaherbivores. Here we present a research approach that explores megaherbivore foraging behavior, and assesses the applicability of foraging theories developed on smaller herbivores to megafauna. With simulation models as reference points for the analysis of empirical data, we investigate foraging strategies of the common hippopotamus (*Hippopotamus amphibius*). Using a spatially explicit individual based foraging model, we apply traditional herbivore foraging strategies to a model hippopotamus, compare model output, and then relate these results to field data from wild hippopotami. Hippopotami appear to employ foraging strategies that respond to vegetation characteristics, such as vegetation quality, as well as spatial reference information, namely distance to a water source. Model predictions, field observations, and comparisons of the two support that hippopotami generally conform to the central place foraging construct. These analyses point to the applicability of general herbivore foraging concepts to megaherbivores, but also point to important differences between hippopotami and other herbivores. Our synergistic approach of models as reference points for empirical data highlights a useful method of behavioral analysis for hard-to-study megafauna.

Keywords: Hippopotamus; Megaherbivore; Spatially explicit; Foraging behavior; Central place foraging

1. Introduction

Herbivore foraging behavior has been studied across a wide size range of organisms from chipmunks to cows (Giraldeau et al., 1994; Laca and Demment, 1990). Few studies, however, have focused on the foraging behavior of a megaherbivore. Empirical research or experimentation on megafauna is often logistically problematic. Despite the highly mobile nature of very large animals, megafauna are extremely sensitive to disturbance and human impacts (Owen-Smith, 1989). As such, megafauna may be vulnerable or prone to extinction. Limited research on basic megafauna behaviors has been an impediment to necessary conservation efforts.

The common hippopotamus (*Hippopotamus amphibius*) is one of the largest terrestrial organisms. Like African elephants (*Loxodonta africana*) and the black rhinoceros (*Diceros bicornis*), hippopotami are megaherbivores that influence natural systems at large temporal and spatial scales, creating a mosaic of habitat for smaller organisms and, at times, altering

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physiognomic habitat structure (Owen-Smith, 1988). Both elephants and rhinoceros forage throughout the day moving across large home ranges; for elephants this can cover an area as large as 25 km^2 (Hall-Martin, 1984). Unlike these megaherbivores, hippopotami (hippos) have strong temporal and spatial constraints on their foraging behavior. Hippos are temporally constrained in that they forage primarily at night (Laws, 1968). Hippos are spatially constrained by their aquatic habitat requirements; a foraging bout begins at a water source and ends at the same or nearby water source (Field, 1970). Despite research spanning more than 30 years (Laws, 1968; Field, 1970; O'Connor and Campbell, 1986; Viljoen and Biggs, 1998), hippo foraging behavior is poorly understood.

Behavioral models can be useful when empirical investigation is prohibitive. Although there is no existing conceptual framework to model hippo foraging behavior, hippos are similar to other large herbivores in that they face a forage environment of patchily distributed, highly variable (in quality and quantity) food. Herbivore foraging theories offer several conceptual constructs that describe a herbivore's response to landscape heterogeneity, variability, and behavioral constraints. The marginal value theorem (MVT) proposes that forage patches are evaluated based on a gain threshold estimated from the average net gain value among patches, assuming searching costs and handling time remain constant (Charnov, 1976). Alternatively, given their spatial constraints, hippos may act as central place foragers, a special case of the MVT in which search costs vary depending on the distance from a central area (Orians and Pearson, 1979; Schoener, 1979). The central place foraging (CPF) theory posits that costs associated with traveling from a central place to a foraging area will influence foraging behaviors, such as selectivity and intake.

Although hippos may not forage optimally, these theories provide several predictions as a framework to interpret hippo foraging behavior. If hippos assess a patch based on an estimated average patch value within a foraging area, we might expect forage patches with resource levels below this average value to be ignored. As central place foragers, hippos may increase selectivity at increasing distances from the central place, in this case, a river. Alternatively, hippos may increase intake rate or reduce search time when farther from a river.

Despite a long history of studies linking theoretical and empirical behaviors (Krebs et al., 1977; Zach, 1979; Kalcenik, 1984), there has been relatively little research to incorporate realistic landscapes context into conceptual explorations of behavior (but see Bernstein et al., 1991; Ruxton, 1995; Baker, 1996; Roitberg and Mangel, 1997; Grünbaum, 1998; Reinhardt, 2002). And yet, for organisms with strong spatial and temporal constraints (e.g. hippos), incorporating a landscape that includes spatial variability in quality and quantity of forage has been shown to be necessary to evaluate behavior in a realistic energetic context (Senft et al., 1987; Laca and Demment, 1991; Turner et al., 1993; Moen et al., 1997; Etzenhouser et al., 1998). Here, we present a spatially explicit foraging model to compare the energetic consequences of several foraging strategies for hippos. The simulation model generated behavioral patterns and energetic outcomes as output. This output was then compared to field observations made on wild hippos. Our approach presents a method of behavioral analysis for hard-to-study species when extensive direct observation or experimentation is not feasible. The model also provides a means of assessing the applicability of traditional herbivore foraging concepts, developed on smaller herbivores, for an unusual megaherbivore.

2. Methods

2.1. Vegetation sampling

The habitat configuration and composition used in the model landscape represents actual dry season (September–November) vegetation around a water source in Katavi National Park (KNP), Southwestern Tanzania, collected in 1995 and 1997. Search and movement rules become more influential when resources are scarce as they are during the dry season. Therefore, behavioral decisions are easier to detect under dry season conditions (Turner et al., 1993). Sampling was based on line transects starting at a water source. The transects followed the paths hippos used nightly to move to foraging areas. Paths were followed and sampled until each trail reached a foraging area or ended. At 50 m intervals along the trails, a quadrat of 25 m × 25 m was measured along either side of the hippo trail. In each quadrat, the percent cover of each grass species, average grass height, percent bare ground, and grass biomass was measured. Initially, biomass (kg/m^3) was measured directly by clipping a 0.25 m^2 area of grass, drying and weighing the grass. Once weighed biomass values were determined and the recorder was trained at visually estimating these values, densities within each measurement zone were visually estimated. Visual biomass estimates were recalibrated by clipping and weighing samples twice monthly. We included seven grass species in this analysis. Although this does not include all grasses observed, these forage species were most frequently encountered along the hippo trails. These are: *Cynodon dactylon*, *Themeda triandra*, *Panicum maximum*, *Sporobolus pyramidalis*, *Echinochloa pyramidalis*, an *Eragrostis* species and a *Digitaria* species. By simulating dry season conditions, we assumed that vegetation within a cell did not regenerate over the time scale of the model; energy gained per cell was only influenced by forage removal.

2.2. Model landscape

The landscape is a grid with 100 m^2 cell size, and represents a 4 km × 2 km area of vegetation adjacent to several hippo pools in a river in KNP. Vegetation characteristics in each cell are based on spatial data collected during dry season months in KNP in 1995 and 1997 (see 2.1 Vegetation Sampling). Vegetation data in each cell included grass species, height, density, and encounter rate. To represent the spatial distribution of hippo pools at the field site, we included two starting points for the simulations (Fig. 1). Starting points represent the place at which the model hippo began the simulation, and were spaced approximately 1200 m apart, roughly equal to the distance between the two major hippo pools at the field site.

2.3. The model

The foraging model is run in Model of Animal Behavior—MOAB (Carter and Finn, 1999), an individual-based simulation model interfaced with a raster-based geographic information system (GIS). The GIS creates locational databases to describe the heterogeneous landscape. For each location, the program stores data on habitat type, resources, and the history of events in each cell. The simulation program incorporates two general behavior types—random walk or dynamic decision-making. The decision-making behaviors are based on a logic-based system that first queries the animal about its internal state variables, and then queries the GIS about associated environmental variables. Behavioral decisions are determined by likelihood algorithms. The likelihood algorithms assign a likelihood, L, for seven behaviors based on the dynamic state variables of the individual and associated environmental factors. The behavior with the largest L is chosen. The simulation includes three foraging-related behaviors: move to a neighboring cell, eat resources in a cell, and stay in a cell, but do not eat. Because foraging behavior dominates the activity budget for hippos when on land at night (Field, 1970), this range of behaviors is realistic. If two neighboring cells have equal food levels, the animal will choose randomly between them

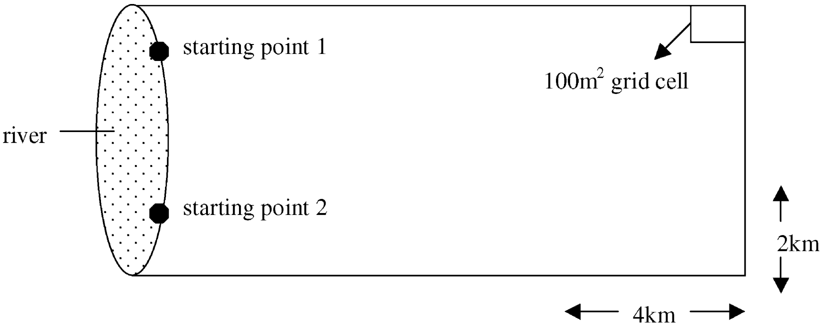

Fig. 1. The model landscape is a grid of cells (100 m^2 per cell) that represents an area (4 km × 2 km) in KNP. Vegetation characteristics in each cell are based on data collected during dry season months in KNP in 1995 and 1997, and included grass species, height, density, and encounter rate. To represent the multiple hippo pools found in this area, model hippos started the simulation at one of two starting points.

(Carter and Finn, 1999). Each simulation followed an individual adult hippo; vegetation removal by other hippos or herbivore species was not included.

The model simulated four foraging scenarios: random search and movement, and three state-dependent behavioral strategies. These state-dependent strategies incorporate forward-biased search and movement—one form of directed, non-random movement (With, 1994). The behavioral strategies we tested are a MVT patch (i.e. cell) threshold, and two CPF strategies: distance-dependent selectivity and distance-dependent intake. In the MVT strategy, the hippo ignores cells with resources that drop below an energetic threshold. We tested three energetic thresholds—an average threshold that is the mean energy available (in kJ) from all cells in the landscape, a threshold one standard deviation above this average, and a threshold one standard deviation below this average. Standard deviations were taken from the distribution of per-cell energy values in the landscape. In the distance-dependent CPF simulations, model hippos either increased selectivity or increased intake at larger distances from the pool.

Large herbivores have been shown to evaluate neighboring foraging patches in addition to the current patch (Gross et al., 1995). To address this, the state-dependent behavioral strategies were simulated at three levels of environmental perception—local, intermediate and full knowledge. Local knowledge assumed the hippo only assessed cells contiguous to the occupied cell. Intermediate knowledge assumed the hippo assessed the environment as far as five adjacent cells in each direction. Full knowledge assumed the hippo assessed ten adjacent cells in each direction.

2.4. Model parameters

Behavioral decisions in the model were based on landscape characteristics and energetic state variables; the model used energy gain as the model currency (sensu Turner et al., 1993). A daily energy balance, computed by subtracting energy costs from energy gained at each time step, was calculated as the sum of all time steps as the hippo moves and forages. At each time step, net energy gain was determined by the gross energy from foraging (kJ/kg) minus energy costs. Energy costs included cost of movement and maintenance (feeding, digestion) per meter, based on published allometric equations (Demment and Van Soest, 1985; Hudson and White, 1985; Alexander and Maloiy, 1989). We assumed walking speed was constant. Dry season energy content of forage was determined from protein and fiber contents, and a digestive efficiency factor based on information from the FAO Animal Feed Resources Information System database (http://www.fao.org/WAICENT/faoinfo/agricult/aga/agap/frg/afris).

Intake was calculated as the product of *bite depth*, *bite area*, *number of bites*, and vegetation biomass. *Bite depth* equaled the vertical dimensions of the vegetation as we assumed that hippos faced no physiological barrier limiting bite depth with vegetation under 30 cm and all grazing areas contain vegetation shorter or equal to 30 cm. *Bite area* was fixed as the product of width of *bite gape* and *bite height* (how wide the mouth is opened vertically). *Number of bites*, or bite rate, represents the average dry season bites per minute. Bite rates were based on direct observations of approximately 200 focal adult individuals that were observed at foraging sites during dry season months (see 2.5 *Field data*). We assumed the dry season functional response of hippos was limited by forage availability. Thus, intake in the model was determined solely by vegetation height and density, as we assumed bite rate was constant in the simulation.

Each simulation run represented an individual hippo foraging for one night, which consisted of eight nighttime hours, with ten-minute time steps. For each simulation, one of four (random, MVT, CPF-selectivity, CPF-intake) behavioral strategies was selected. In addition, for the three state-dependent behavioral strategies, one of three levels of environmental perception was chosen (local, intermediate, full). Each parameter combination was run for 100 simulations. The model outputs measured distance traveled, which was defined as the square root of the sum of travel in the x direction squared and travel in the y direction squared; gut fill (kg); net and gross energy gained (kJ); search efficiency, defined as the ratio of gross energy gained to total distance traveled; and foraging efficiency, defined as the ratio of net energy gained to gut fill. To evaluate field data and compare energetic output among the three models, we used one-way, fixed effects analysis of variance (ANOVA), analysis of covariance (ANCOVA) and regression models, after testing that the data complied with model assumptions and accounting for correlations between independent variables. We also used likelihood estimation and a goodness-of-fit chi-square framework to compare model output to field observations (Hilborn and Mangel, 1997). We compared model-predicted intake rates at foraging sites in the model landscape to field-observed foraging behavior at corresponding field sites using likelihood estimation. We transformed intake values by taking the log function (ln(intake value)). The likelihood function determines the probability of observed values given a particular model calculated as:

$$L = \prod_{j=1}^{J} \frac{1}{\sigma_{ik}\sqrt{2\pi}} \exp\left[\frac{-(R_{ij} - m_{ik})^2}{2\sigma_{ik}^2}\right] \qquad (1)$$

where σ_{ik}, σ_{ik}^2, m_{ik} are the standard deviation, variance and mean of intake rates from model k at site i. R_{ij} is the field-observed intake rate of animal j at the corresponding field foraging site i. Foraging patterns among foraging areas predicted in the model were compared to foraging patterns from field observations using a goodness-of-fit framework:

$$\chi_k^2 = \sum_{i}\sum_{N}\left(\frac{(\phi_{ik} - f_i)^2}{\phi_{ik}}\right) \qquad (2)$$

where f_i is the fraction of field-observed hippo foraging visits at site i, N is the total number of field observations, and ϕ_{ik} is the fraction of model foraging visits to site i for model k. Goodness-of-fit was determined by the model that minimized this value. Statistical tests were performed using STATISTICA (Statsoft, 1984).

2.5. Field data

Field data were collected at foraging sites represented in the model landscape during dry season months in 1995 and 1997. Data were collected during nighttime hours from a parked vehicle using a Javelin nightscope (Model, 223). Focal adults were chosen randomly and observed for 3–5 min periods. If multiple observations were made on the same focal animal, values were averaged across observations. Because individual identification was impossible, data between foraging areas over time may not be independent. However, with 500–800 hippos in the study area, confounding effects of data dependence are unlikely. Lactating females and juveniles were excluded from this dataset. Number of bites and steps per minute, and time were recorded during each observation period. The vegetation height, biomass, composition, and distance to pool also were measured at each foraging site. We assumed step rate was an indication of search time and that less search time in an area would result in higher intake rates (Laca and Demment, 1991).

3. Results

3.1. Comparing model output

The random behavior simulations were not able to meet the metabolic requirements set as the simulation parameters—all runs resulted in zero (or values not significantly different than zero) net energy gained, despite foraging during the runs. The CPF strategies generally outperformed the MVT strategy based on significantly higher net energy gains, and higher search and foraging efficiency for both starting point configurations (ANOVA, Point 1: $F_{2,540} \geq 11.9$, $P < 0.001$; Point 2: $F_{2,540} \geq 15.1$, $P < 0.001$). Net energy gained was at least 30% higher for CPF strategies. Between the two CPF strategies—distance-dependent selectivity and distance-dependent intake—distance-dependent intake resulted in higher net energy gained (about 10% higher), and higher search efficiency (ANOVA, $P < 0.02$). The two CPF strategies performed equally well in terms of foraging efficiency. The range of patch thresholds (energy levels below which a patch is ignored) used to evaluate the MVT strategy did not significantly influence energy gained, or efficiencies of simulation runs for the MVT strategy, although the thresholds covered a broad range of forage resources within a cell (total cell average ± 1 S.D.).

For both starting points, the level of knowledge the hippo had about its foraging arena had a significant effect on the net and gross energy, search efficiency, and foraging efficiency. Both intermediate and full knowledge yielded 40% higher energy gains than local knowledge (ANOVA, $P < 0.001$). However, neither intermediate nor full knowledge were consistently superior to the other across these simulations.

To identify which parameters most strongly influenced net energy gained for the most successful

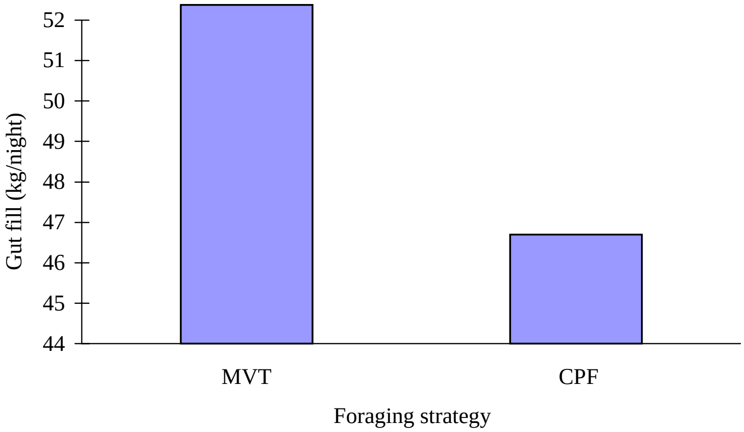

Fig. 2. Comparison of gut fill between MVT and CPF strategies across simulations with comparable net energy gained.

strategies, we tested model parameters using multiple linear regression. For the CPF strategies, net energy gained was explained primarily by search efficiency (β-coefficient = 0.65) but a model with both search and foraging efficiency (β-coefficient = 0.20) accounted for more of the observed variation than either variable alone ($r^2 = 0.65$, $P < 0.02$). We also considered the influence of forage quality on the components of foraging efficiency, our measure of foraging performance. The proportion of high quality food was negatively correlated to gut fill, the denominator in the foraging efficiency measurement ($r = -0.83$, $P < 0.05$). Gut fill was higher for the MVT strategy than the CPF strategies (Fig. 2), although these differences were not statistically significant.

3.2. Field data

We then asked whether there was evidence in the field data to support the trends and patterns identified by the model simulation comparisons. In the field, there was also little evidence of MVT thresholds at the patch level as at least 50% of foraging occurred at foraging sites with the lowest vegetation biomass and height. There was, however, evidence of CPF strategies. Across 202 focal animal observations, there were significantly higher bite rates at foraging sites farther from the pools (logistic regression, $r^2 = 0.33$, $P < 0.001$), suggesting distance-dependent variation in intake (Fig. 3). This follows a CPF prediction that intake rate in a patch should increase with increasing distance from the central place (Orians and Pearson, 1979). However, the relatively low r^2 value associated with this regression model suggests that intake is influenced by other factors. Further analyses implicated other vegetation characteristics; hippo foraging behavior also responded to changes in vegetation quality. By grouping the seven forage species into two quality categories (high versus low) based on energy content (kJ/kg), we found that vegetation quality, with biomass as a covariate, was significantly associated with higher bite (ANCOVA, $F_{1,159} = 8.72$; $P < 0.004$) and lower step rates (ANCOVA, $F_{1,159} = 7.86$; $P < 0.006$) (Fig. 4). Lower step rates indicate less searching and, thus higher intake rates at that site. There was, however, no detectable response to biomass when considered alone. Hippo bite rate appeared to be insensitive to dry season biomass (Fig. 5).

3.3. Comparing model results to field data

We used two tests to compare model results to field data. Likelihood estimates compared model-predicted intake rates at model foraging sites to field-observed intake rates at corresponding foraging sites in the field. The intake rates predicted by the distance-dependent intake CPF strategy generated the most comparable values when compared to the observed intake rates from the field (Table 1). The second comparison was a goodness-of-fit to test the similarity of percent of time

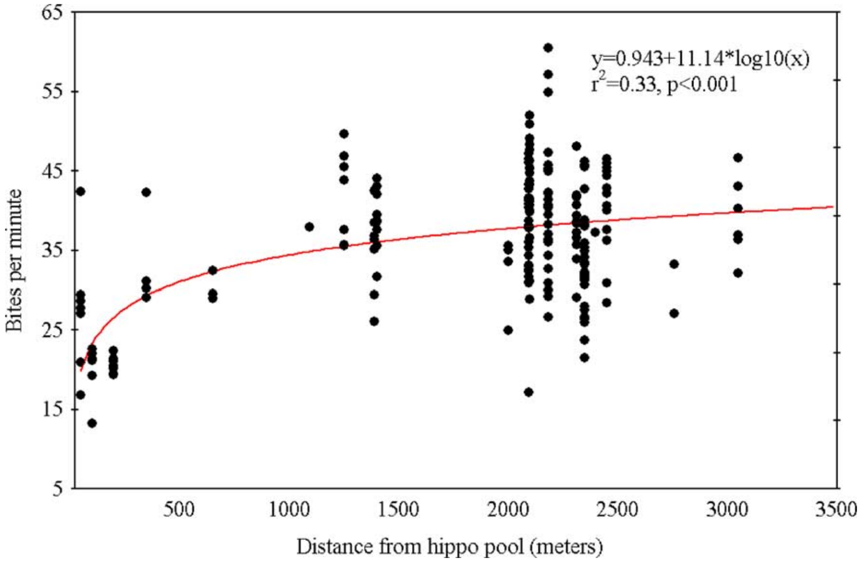

Fig. 3. Bites per minute as a function of the distance from the hippo pool, based on 202 focal individual observations. Because individual identification was not possible, data points may not be independent (see 2.5 *Field data*).

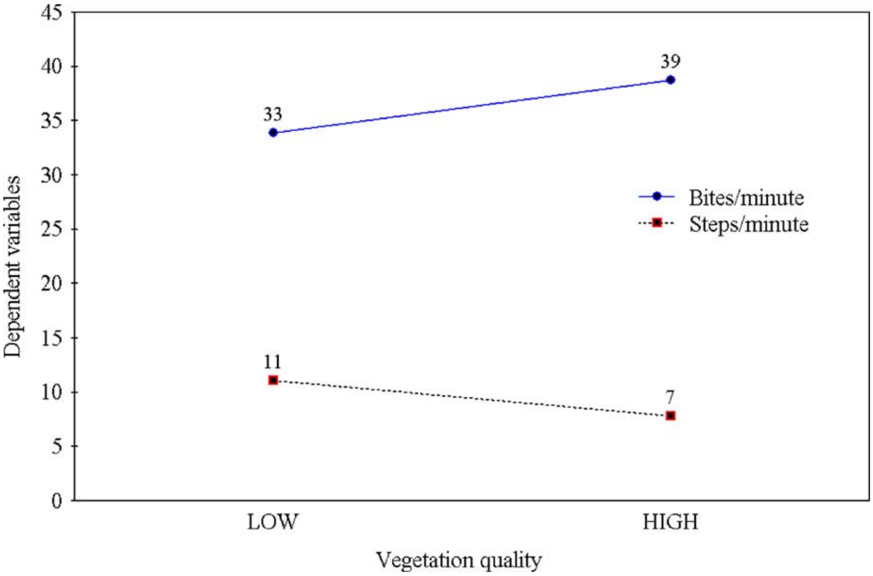

Fig. 4. Relationship between vegetation quality and foraging behavior. Data points were split into two vegetation quality groups, low and high, based on energy content (kJ/kg). High quality vegetation included *Cynodon dactylon*, *Echinochloa pyrimidalis*, *Panicum maximum*, and a *Digitaria* species. Low quality included *Themeda triandra*, *Sporobolus pyrimidalis*, and a *Eragrostis* species. The high quality vegetation had significantly higher energy content (Kruskal–Wallis ANOVA, median test, $P = 0.047$) Mean bite rate increased and step rate decreased at foraging sites with higher quality vegetation.

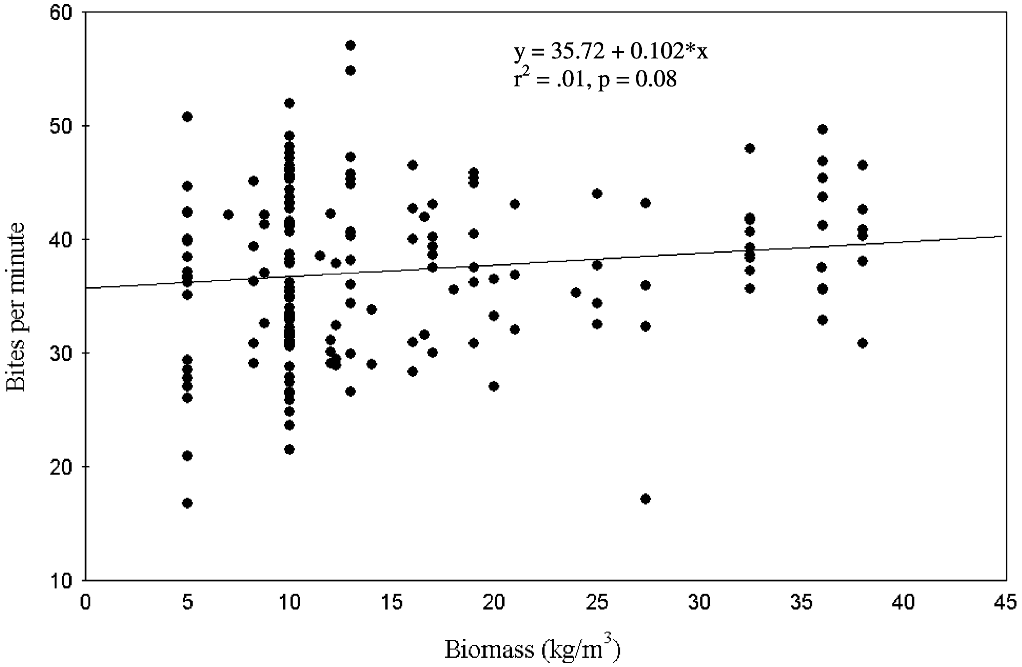

Fig. 5. The relationship between bite rate and dry season biomass.

spent foraging at five major foraging sites predicted by the models and observed in the field. We found no statistical difference in model-predicted movement patterns among the three strategies for starting point 1. However, for starting point 2, field movement patterns were best fit by output from the distance-dependent intake model (χ^2 values = 0.10 distance-dependent intake; 1.4 distance-dependent selectivity; 2.27 MVT) (Fig. 6).

Table 1
Negative log-likelihoods comparing model-predicted intake rates at foraging sites in the model landscape to field-observed foraging behavior at corresponding field sites for three behavioral strategies (CPF DDI—distance-dependent intake; CPF DDS—distance-dependent selectivity; MVT—marginal value theorem)

	CPF DDI	CPF DDS	MVT
Model starting point 1	−9.24	−13.15	−13.41
Model starting point 2	−17.10	−56.47	−60.61

All intake values were log transformed. The likelihood function determines the probability of observed values given a particular model. Starting points represent the location at which the model hippo began the simulation. Multiple starting points were included to represent the distribution of hippos in the river at the field site.

4. Discussion

In simulation models comparing four foraging strategies (random, MVT, CPF-intake, CPF-selectivity), we found that non-random foraging strategies yielded higher foraging success (sensu Moen et al., 1997; Turner et al., 1993). Of the state-dependent behavioral strategies, the CPF strategies, in which distance from the river influenced foraging decisions, were the most energetically effective. The CPF-intake strategy, in which the simulated hippo increased intake when farther from the river, was the most effective in terms of net energy and search efficiency. In addition to the energetic success of the CPF strategies, these strategies also yielded lower levels of gut fill than MVT for comparable levels of energy gained. Although not statistically significant at the temporal scale of the simulation (one night), the difference of 5 kg per day may be biologically significant at longer time scales. Hippo's daily intake and gut capacity per body weight is lower than other megaherbivores of comparable size, which most likely stems from relatively long gut retention times (Van Hoven, 1982; Owen-Smith, 1988). Because of the limits to gut

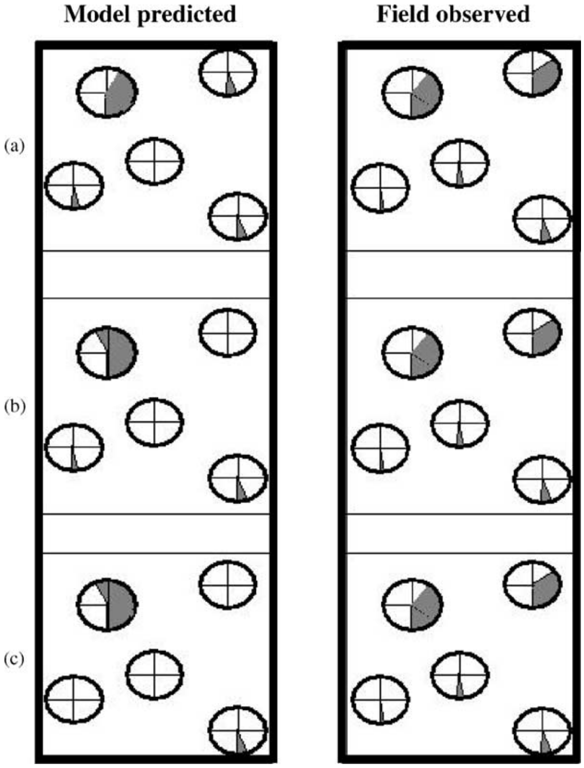

Fig. 6. Goodness-of-fit between model predicted (starting point 2) and field-observed movement patterns. Each circle represents the percent of time spent foraging at five major foraging sites. The proportion of the circle shaded represents the percentage of foraging visits that occurred at each site predicted by the models (left column) and observed in the field (right column). Rows represent behavioral strategies: (a) CPF distance-dependent intake, (b) CPF distance-dependent selectivity, (c) MVT.

capacity, a high ratio of kJ/kg may be a necessary component of an effective hippo foraging strategy.

We also found evidence of CPF behavior from field observations. Wild hippos were found to increase bite rates, one measure of intake, when foraging farther from the river, a finding consistent with CPF predictions. Hippo foraging behavior also responded to vegetation quality across all foraging sites; bite rate was higher, and step rate, a measure of time spent searching, was lower. Although hippos do not conform to the CPF theory as it was initially described—a foraging bout with selection of prey or a patch followed by an immediate return to the central place—our model and field results suggest that the CPF spatial construct provides a useful framework for hippo foraging behavior. Thus, some foraging models and theories developed for and tested on smaller herbivores can apply to a megaherbivore.

We have also identified important differences between hippos and other herbivores. Most notable is the response of intake to vegetation quantity, or biomass. Whereas studies on smaller herbivores have described a monotonic increase or decrease in bite rate in response to increasing vegetation biomass (Demment and Greenwood, 1988; Bradbury et al., 1996), hippo bite rate appears to be insensitive to dry season biomasses alone. This may be a function of the relatively small range of dry season vegetation heights (and thus biomasses) that hippos can utilize due to physiological constraints on horizontal neck movement. It is also possible this difference derives from a true difference between hippos and smaller herbivores; field observations yielded no evidence of cropping or handling time, i.e. hippos appear to chew and bite continuously while foraging (R. Lewison, personal observation). Traditional foraging concepts define prey quality as a ratio of net energy gained to handling and search time. The putative absence of handling time for hippos and the significant effect of distance from the central place suggests that vegetation is evaluated based solely on energy available (quality) and search time, defined as distance to the river.

4.1. Caveats

This model provides a realistic energetic background to explore hippo foraging behavior. Yet, there are elements of hippo physiology and life history not captured in the model. Our simulations only consider dry season conditions; there may be different foraging strategies employed during wet season months. Non-lactating adult hippos are thought to forage independently (Field, 1970), however, there may be an influence of conspecifics not captured by this model as only one individual was followed per simulation (Giraldeau et al., 1994). Given the likely importance of retention time, a hippo foraging model that explicitly includes digestion and passage of forage through the digestive tract would likely be more realistic, but would require detailed information on digestive physiology. In addition, like all models, we assume our chosen model currency confers fitness benefits, i.e. higher net energy gained results in higher fitness. Previous authors have demonstrated that energy (per unit time) maximization is not the only currency critical to herbivores (Belovsky, 1978; Lima et al., 1985; Holmes, 1991). However, given their few non-human predators and gross level of plant part selection, it is likely that net energy is a plausible currency for hippos. We also did not include all energetic costs wild hippos are likely to face; our models incorporated energetic costs associated with foraging, but did not include additional costs of growth and reproduction.

The model was designed to recreate the observed patterns of hippo foraging (Field, 1970; O'Connor and Campbell, 1986). Thus, the simulated hippo left the water source, foraged in the landscape, and returned to the starting point. This construct may have introduced a bias in model results to favor the CPF strategy. However, this potential bias would not have influenced the patterns from field observations, nor would it have influenced model-field comparisons. The patterns observed in wild hippos (Figs. 3–5) represent foraging behavior in over 200 putative individuals. Thus, the behavioral changes observed in the empirical data account for both the signal (response to vegetation quality and distance) and the noise inherent from individual variation. The significant changes in bite and step rate as a function of distance from the river and vegetation were reported on a shorter time scale (per minute) and are likely to become more influential over longer time scales. Likewise, the daily differences observed in gut fill between foraging strategies in the simulation model may become more important over weeks or months.

Finally, although the two starting-point configurations yielded similar qualitative patterns, we found quantitative differences. The differences between two starting point configurations highlight the difficulty in characterizing hippo foraging behavior with 'snapshots' of foraging behavior that can be gleaned from direct observation at foraging sites. Without technological improvements, such as telemetry, it will be impossible to fully describe foraging behavior of hippos from the start of the foraging bout to the finish. These technological advancements have been critical for research on other megaherbivores (Stuwe et al., 1998; Blake et al., 2000), but have yet to be pursued for hippos.

5. Conclusions

The primary goal of the model presented here was to evaluate the energetic ramifications for hippos from well-known herbivore foraging strategies and to compare model output to field data from wild hippos. Our results suggest that hippos conform to general CPF predictions. We evaluated model strategies based on a suite of outputs—net and gross energy gained, search and foraging efficiency, total distance traveled from the water source, and gut fill. CPF strategies were found to be most effective in terms of these outputs. Field-observed hippos also responded to vegetation quality and distance from the river, increasing bite rate and decreasing step rate at higher quality foraging sites and increasing intake when foraging farther from the river. Although the goodness-of-fit and likelihood estimation measures were relative comparisons, i.e. not an absolute measure of how accurately a particular model represented empirical observations, the distance-dependent intake CPF strategy, in which the model hippo increased intake rates at larger distances from the river, was consistently congruent with field data. Unlike some other herbivores, hippo foraging was not responsive to biomass alone. It is unclear whether this is a function of the relatively small range of dry season biomasses or the absence of cropping or handling costs. This supports Spalinger and Hobbs (1992) who found that functional response is a dynamic function of both plant density and mechanics of cropping and processing by the herbivore.

Understanding hippo foraging behavior has conservation implications. Hippo populations are believed to be declining in many African countries and the geographic range of this species across the African continent is contracting, primarily due to loss of habitat (IUCN, 1993). In densely populated countries, like Kenya and Malawi, human fatalities from hippopotamus attacks and incidence of hippo crop raiding have increased in developed regions adjacent to protected areas (Mkanda, 1994; KWS, 1996). This model presents one approach to tackle these issues. Although some results of this analysis may be site-specific, the model also points to the general importance of buffers around protected areas (Newmark, 1985; Wilcove and May, 1986; Shafer, 1990; Forman and Moore, 1991). Natural boundaries, such as lakes and rivers, are commonly used to delineate protected areas (Hunter, 1996). If hippos are active throughout the boundary lake or river, and human densities are high outside the boundary, these unbuffered natural boundaries are likely to intensify human-hippo conflicts. Utilizing a CPF construct, we have identified patterns of hippo habitat selection and foraging behavior, albeit at a coarse resolution (Rosenberg and McKelvey, 1999).

One challenge to behavioral ecology is the development of conceptual or theoretical models that are relevant to animals in natural systems (Lima and Zollner, 1996). Incorporating a meaningful context for behaviors, i.e. the landscape, is an important component to this relevance. Our model simulated hippo foraging behavior from several foraging strategies in a real-world landscape, in this case created with field data in a GIS. Such spatially explicit models contextualize behavior, and can incorporate dynamic behavioral decision rules that are contingent on a spatially heterogeneous landscape (Turner et al., 1994; Roitberg and Mangel, 1997). For hippos, this type of model yielded some mechanistic understanding of foraging decisions by connecting conceptual models to the hippo's ecological landscape. Our approach of using conceptual models as a framework to interpret empirical data can be a useful tool to explore the behaviors of hard-to-study megafauna.

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