



MIAMH, A Predictive Model of Range Ruminant Diets in Patchy Environments

Didier Genin^a & Roberto Quiroz^b

^a Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), C.P. 9214, La Paz, Bolivia

^b International Development Research Center (IDRC), Casilla 12304, San Miguel, La Paz, Bolivia

(Received 23 June 1992; accepted 26 November 1992)

ABSTRACT

A utilitarian simulation model of botanical composition of ruminant diets on rangelands is proposed. It emphasizes the use of forage resource diversity within the range ecosystem context. The forage species, within a plant community, are taken as the functional unit of the model. Four indices are defined: (a) a probability of encountering forage i in the plant community, (b) a structural index of bite taken in forage i , (c) a quality index of forage i , and (d) a selectivity index of the animal foraging. These indices are combined to calculate potential alimentary capacities of forage species (PAC), and to estimate their contribution to the diet taken from a particular plant community. An extrapolation to the overall habitat is then made, by an estimation of relative feeding times spent within the various plant communities of the rangeland.

INTRODUCTION

Numerous studies have dealt with diet selection of domestic and wild ungulates. Their concern has been essentially with the description of composition of diets selected by specific animals within specific environment. In comparison, very few researchers have investigated the foraging process, which is perhaps the single most important aspect of understanding plant-animal interactions (Crawley, 1983).

The most common conceptual approach to the foraging process is optimal foraging theory (Schoener, 1971; Belovsky, 1978). Several problems



are found in its application to large herbivores, because these animals confront an apparent food surplus, which is of low and highly variable nutritive quality spatially and temporally (Senft *et al.*, 1987; Coughenour, 1991), and of wide physical heterogeneity (McKell, 1989). Nutrition-based optimization models lead generally to estimations of low plant diversity in the diet composition of large herbivores (Westoby, 1974; Pullim, 1975; Belovsky, 1978). These results are contrary to observations (Westoby, 1978; Maizeret, 1988).

Factors affecting diet selection by large herbivores are numerous and located at various ecological scales (Senft *et al.*, 1987; Stuth, 1991). It is very difficult to determine exhaustively how a particular factor at each scale links to others. Modelling could be a useful tool in the formulation of hypotheses on the main determinants of diet selection, and could, therefore, have applications in evaluating rangeland utilization and management practices.

Several simulation models have been proposed for large herbivores grazing on rangelands, but they usually concern herbaceous communities and very few emphasize diet selection (Van Dyne *et al.*, 1980). This is taken into account as input data of forage species palatability indices (Goodall, 1969; Rice *et al.*, 1986; Orsini, 1990), a measure of plant digestibility (Freer *et al.*, 1970; Sibbald *et al.*, 1979), or a result of green forage availability (Van Dyne, 1969; Arnold & Campbell, 1972). In the case of mixed plant communities, their physical, phenological and chemical diversity mean that plant digestibility and green forage availability are not always correlated with food selection (Vangilder *et al.*, 1982). Palatability is an *a posteriori* descriptive parameter which summarizes food selection, but which does not approach its functional aspects. Our model of herbivore diet selection will generate hypotheses about the major factors concerned with plant preference in a given environment. Stuth (1991) indicated that the preference status of a particular plant species is largely dependent upon its inherent abundance, its morpho/phenological characteristics, the array of species on offer, and the species of animal in question. In this sense, Ellis *et al.* (1976) presented a conceptual model of diet selection as an ecosystem process in which four major factors are distinguished: (1) the food requirements of the consumer, (2) food availability, (3) consumer preferences for particular kinds of food, based on past experience, and (4) the selectivity of the consumer, depending on current nutritional and satiation states. Nevertheless, these researchers did not explicitly state the functional relationships between these components that could lead to a prediction of diet selection.

MIAMH (Modèle d'Information Alimentaire en Milieu Hétérogène) is an operational simulation model of diet selection. It emphasizes the use

of forage diversity within the range ecosystem. A single forage species is taken as the fundamental unit of the model. Various ecological scales and animal factors are considered in the model.

GENERAL DESCRIPTION OF THE MODEL

MIAMH has been conceptualized for goats browsing shrubby vegetation extensively, but its general basis could be applied to any generalist herbivore grazing on diversified rangelands. MIAMH results from a combination of five indices related to the structure of plant communities that form the rangeland; the physical and chemical structure of plant parts to be selected; and a selectivity index of the animal, depending on the animal's characteristics, nutritional needs and the relative quality of the range (Fig. 1).

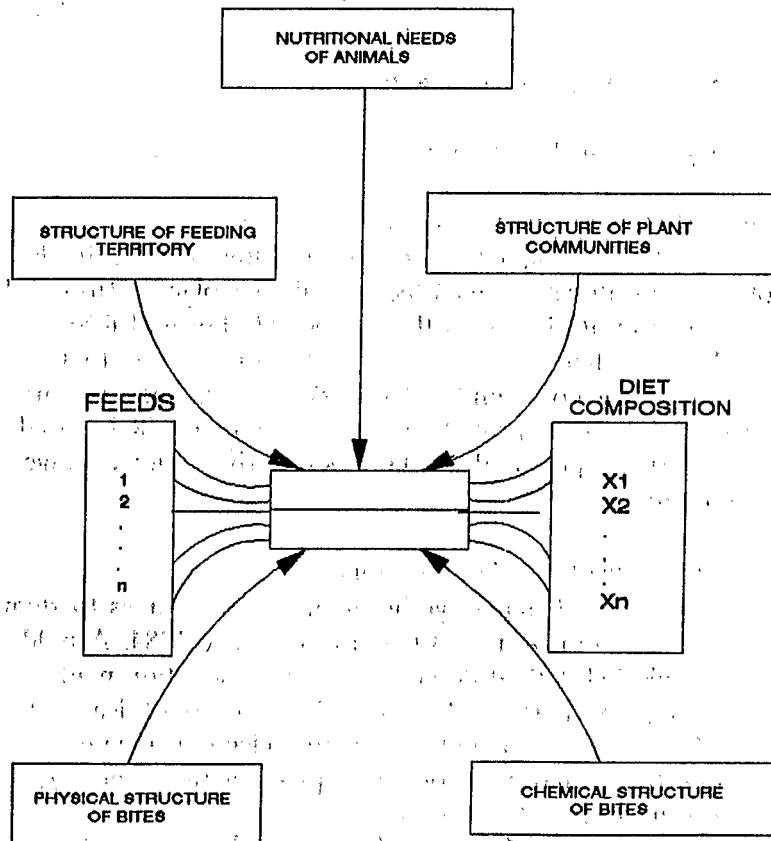


Fig. 1. Organigram of the model MIAMH.

MIAMH is generally based on the concept of 'matching', where animals adjust their foraging behavior to changing dietary rewards (Staddon, 1983; Senft, 1989). The model has modified this behavioral pattern by incorporating characteristics of feed resources and nutritional requirements of foraging animals.

The model follows several concepts of Senft's model (1989). Unlike Senft's model, MIAMH is completely 'a priori'. The model does not need any animal behavior input to run.

MODEL STRUCTURE AND EQUATIONS

The simulation of diet composition is carried out on a daily basis. The calculation is divided into two steps. The first determines the botanical composition of the diet selected within a particular plant community. The second, at a larger scale, determines the total diet composition selected from all plant communities within the rangeland per day.

Diet selection within plant community j

Five indices are defined, as follows.

Probability of encounter with food type i

On the range, the feeding activity of the consumer can be divided into a series of feeding stations at which the animal bites plants (Ruyle & Dwyer, 1985; Demment *et al.*, 1987). In the absence of choice of feeding station, the probability of finding the forage i , R_{ij} , corresponds to the relative frequency of i in the community j (Belovsky, 1981). The frequency of i is from cover data. These probabilities of encounter will be used in the model to determine potential availabilities of the various forage species of the community.

Physical index of the bite taken on forage i

Several studies showed that large herbivores prefer leaves to stems, and green (or young) to dry (or old) material (Leclerc, 1984; Arnold, 1985). Pfister and Malechek (1986) described the wide selection made by sheep and goats on plant parts and proposed the ratio of leaves to stems weights within a bite as an index of plant selection. Genin and Badan (1991) demonstrated that goats preferred plants with flowers and fruits in the coastal scrub of Baja California.

The structural composition of the bites taken by a particular species or class of herbivore can be characterized by its mouth characteristics, the

type of prehension, and its physiological state (Hanley, 1982; Arnold, 1985). These variables appear to influence the choice of forage species.

We define a physical index, P_{ij} , of the bite taken on the species i by a given category of animal as follows:

$$P_{ij} = \frac{\text{weight of leaves and reproductive organs}}{\text{total weight of the bite}} \quad (1)$$

Field observation of bites taken on the various forages can be made to estimate bite weights and structure (Stobbs, 1973).

Quality index

We define a quality index, Q_i , of the bite taken on forage i as the ratio

$$Q_i = \frac{\text{crude protein content}}{\text{lignin content}} \quad (2)$$

This index is based on the fact that diets of large herbivores generally indicate higher crude protein content than the mean crude protein content of forages on offer (Arnold, 1985). Additionally, lignin content is one of the best simple indicators of forage organic matter digestibility (Van Soest, 1982; Lachaux *et al.*, 1987).

Selectivity index of the animals

Following Demment *et al.* (1987), we hypothesize that consumers will effectively try to maximize their nutrient flow, but with more or less 'determination' according to their metabolic needs and the relative quality of plant parts to be consumed from forages of the plant community j . We then define a selectivity index, S_j , of the animal in community j as follows:

$$S_j = \frac{\text{minimum crude protein concentration of diet necessary to satisfy the nitrogen needs of the animal}}{\text{mean crude protein content of forages of plant community } j} \quad (3)$$

This selectivity index is dependent upon the plant community in which the animal is grazing. The index balances the absolute quality index of a forage and the relative needs of animals foraging in community j . It also influences the importance given to the relative abundance of species in the selected plant community. For example, in a nutritional poor community, where $S_j \gg 1$, we assume that animals will prefer and seek good-quality forages, and that the relative abundance of a forage will not be a major factor in its consumption.

General equation

We define the potential alimentary capacity, PAC_{ij} , of species i in plant community j as

$$PAC_{ij} = R_{ij}^{1/S_j} \cdot P_{ij} \cdot Q_i^{S_j} \quad (4)$$

where R_{ij} is the probability of encountering species i in community j , S_j is the selectivity index of the animal in community j , P_{ij} is the physical index of the bite taken on species i and Q_i is the quality index of the bite taken on species i .

A multiplicative model was chosen because it allowed a strong discrimination of the alimentary capacities of different forages. The model also appeared to be more consistent with the notion that feed selection is based on multiple cues acting simultaneously (Senft, 1989). For example, a plant species can be very interesting nutritionally (Q_i high), but if it is rare in the plant community its PAC_{ij} will be low.

S_j is used as an exponent for Q_i because it is assumed that a herbivore effectively tries to maximize nutrient intake (Owen-Smith and Novellie, 1982), but with more or less accuracy depending upon the balance between its nutritional needs and the global quality of the foraged plant community. Similarly, the importance of R_{ij} value for determining PAC_{ij} will inversely depend upon the accuracy of the herbivore to seek plants with the highest nutritional quality. The model promotes then fluctuating hypothetical foraging behaviors, depending upon the characteristics of forage resources of the community in which the herbivore forages, varying from undermatching to overmatching (Staddon, 1983; Senft, 1989). This allows a number of different foraging scenarios, as a function of the characteristics of forage resources.

As an illustration, we assume that a herbivore foraging in a nutritional poor plant community ($S_j \gg 1$), will seek primarily plants possessing high nutritional quality ($Q_i^{S_j}$ high). We also assume the herbivore will be less influenced by the abundance of forages (R_{ij}^{1/S_j} moderate to low) within the community.

The theoretical contribution of species i to the diet selected in the plant community j , TCD_{ij} (in per cent), is derived easily from eqn (4):

$$TCD_{ij} = PAC_{ij} / \sum_i PAC_{ij} \quad (5)$$

Total diet composition

We determined the relative grazing time spent by animals in the various plant communities of the rangeland, RGT_j , as a function of the relative

potential alimentary capacities of the communities in question, $RPAC_j$, and of their relative areas, RA_j :

$$PAC_j = \sum_i PAC_{ij} \quad (6)$$

$$RPAC_j = PAC_j / \sum_j PAC_j \quad (7)$$

$$RA_j = A_j / \sum_j A_j \quad (8)$$

where A_j is the area of community j , and

$$RGT_j = RPAC_j \cdot RA_j / \sum_j (RPAC_j \cdot RA_j) \quad (9)$$

The theoretical contribution of species i to the total diet, TCD_i , is then

$$TCD_i = \sum_j (RGT_j \cdot PAC_{ij}) / \sum_j \sum_i (RGT_j \cdot PAC_{ij}) \quad (10)$$

Inputs and outputs

MIAMH inputs are:

- probability of encounter with forage i , i.e. its relative abundance;
- weight of bite taken on forage i ;
- weight of leaves and reproductive organs contained in the bite taken on forage i ;
- crude protein content of bite taken on forage i ;
- lignin content of bite taken on i ;
- crude protein concentration of the diet necessary to satisfy metabolic needs of the animal;
- relative surface area of plant communities forming the rangeland actually used by consumers.

MIAMH outputs are:

- theoretical contributions of forages to the diet selected in the various plant communities of the range;
- relative grazing times spent by the animals in the plant communities;
- theoretical contributions of forages to the total diet.

TESTING THE MODEL

The model was tested against data from a feeding behaviour study of goats browsing in the coastal scrub of Baja California, Mexico, described by Genin (1990), Genin and Badan (1991) and Genin and Pijoan (1993).

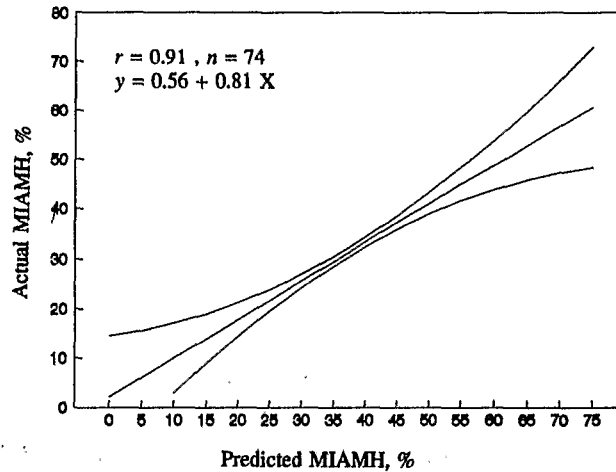


Fig. 2. Confidence band ($P < 0.05$) for the regression of observed species contributions to goat's diet (in per cent) on that predicted by MIAMH.

Vegetation is of a semi-arid type, including a broken layer of drought-deciduous and evergreen shrubs, succulents, and annual grasses and forbs. Four homogeneous plant communities were identified in the feeding territory of goats. The model has been tested for three typical feeding periods in this environment: wet, transition and dry (Genin & Pijoan, in press). Eight shrub species and a mixed group of annual herbs, representing more than 85% of the diet throughout the year, were used

TABLE 1

Actual and Simulated Relative Feeding Time Spent by Goats in Four Plant Communities of the Coastal Scrub of Baja California (in per cent)

	Simulated data	Actual data
Wet period		
Community I	14.2	9.5
Community II	27.3	27.4
Community III	32.9	39.2
Community IV	25.6	24.9
Transition period		
Community I	16.2	17.3
Community II	21.7	25.3
Community III	39.3	32.7
Community IV	22.8	21.1
Dry period		
Community I	13.2	11.8
Community II	14.9	16.3
Community III	49.0	48.5
Community IV	22.9	25.1

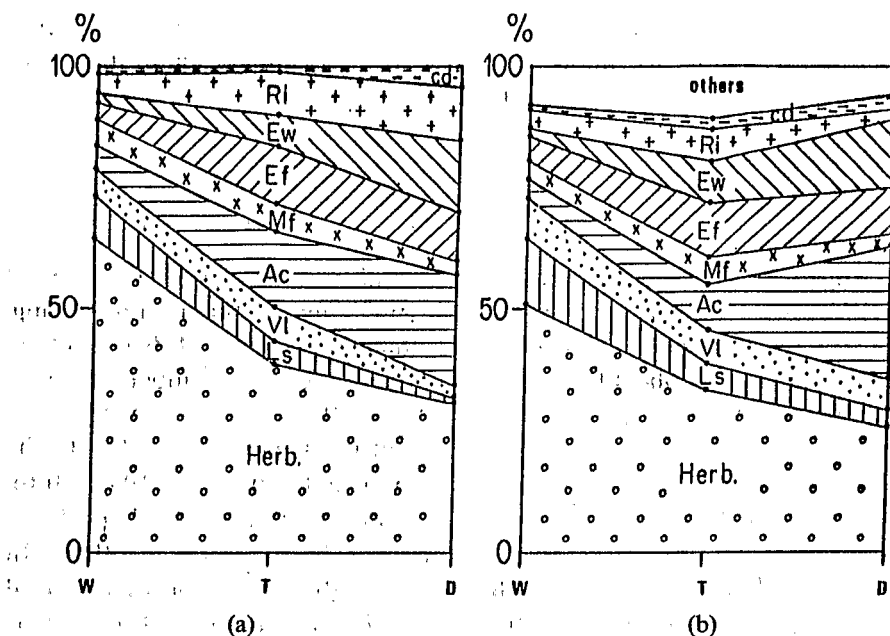


Fig. 3. Total diet composition of goat in the coastal scrub of Baja California during wet (W), transition (T) and dry (D) period. (a) Simulated by MIAMH; (b) actual. Herb, herbs; Ls, *Lotus scoparius*; Vl, *Viguiera laciniata*; Ac, *Artemisia californica*; Mf, *Malacothamnus fasciculatus*; Ef, *Eriogonum fasciculatum*; Ew, *Eriogonum wrightii*; Ri, *Rhus integrifolia*; Cd, *Cneoridium dumosum*; others, other plants.

to run the model. Details of data used have been presented elsewhere (Genin, 1990).

For the three periods, the TCD for the nine forages selected by goats in the four plant communities were highly correlated with the observed contributions to diet ($r = 0.91$, $n = 74$, $RSD = 6.1$) (Fig. 2). The root mean squared error (RMSE), defined as the square root of the mean of the sum of squares of the differences between observed and predicted values, was 6.99%. The RMSE indicates the actual size of the error produced by the model from the particular set of inputs used. Simulated relative times spent in the four plant communities during the three feeding periods are presented in Table 1. They show a correlation coefficient with the observed data of 0.90 ($n = 12$). Estimations of the theoretical contributions to the total daily diet of the main forages are shown in Fig. 3. The spectrum of the goats' diet in the coastal scrub of Baja California has been simulated adequately. Nevertheless, contributions of herbs to diet were overestimated for the three feeding periods, whereas other forages, e.g. *Lotus scoparius*, were underestimated. It is difficult to attribute this distortion to any particular parameter of the model. Contributions to diet of species of low probability of encounter appeared to have been

underestimated. This would support the assertion of several workers that rare species would be more attractive for consumers than dominant species (Le Houerou, 1980; Arnold, 1985).

DISCUSSION

The objective of this work was to try to find functional and/or empirical bases for range herbivore diet selection by preliminary utilitarian modelling. This required simple formulation of hypothetical processes of diet selection, which could be applicable using a relatively reduced number of easily available parameters. We tried to integrate the current knowledge of tactical aspects of diet selection of generalist herbivores, specifically the ecological dimension of the diet selection process (Senft *et al.*, 1987; Stuth, 1991). Nevertheless, some simplifications, approximations and hypotheses were used in the present case, which may not be operative in others. In particular, for the extension of the model to the prediction of the total diet ingested, we hypothesized that the behavioural pattern of animals is matching (Staddon, 1983). These approximations gave good results for goats browsing in the coastal scrub of Baja California, because of the broken mosaic of plant communities forming their feeding territory. In other situations, several additional factors—such as slope, distance to water, penetrability of plant communities and animal management—can strongly influence spatial patterns of animal behaviour (Senft *et al.*, 1983, 1985).

The descriptors selected in the model for evaluation of the potential alimentary capacities of plants can be grouped into four sets of factors which influence diet selection and have to be considered simultaneously: abundance, physical aspect and nutritional quality of feed resources, and relative selectivity of animals (Sibbald *et al.*, 1979; Owen-Smith & Novelie, 1982). If they are easy to collect, these descriptors sometimes have a low precision. For example, crude protein content is a rough descriptor of nutritional quality of range forages (Cooper *et al.*, 1988). These descriptors could be refined in future.

Finally, in its actual state, the model allows a static prediction of diet (for a day or a period). It will have to be integrated in a dynamic model because herbivore-vegetation relationships are always related to flow problems: Time and forage matter flows will have to be considered in the algorithm. Preliminary to this, eventual relationships between bite weights taken by a category of animals and structure of forages consumed, such as those found by Meuret (1989) on oak browsed by goats, could efficiently enhance the qualitative estimations of diet composition provided by MIAMH.

APPLICATIONS OF THE MODEL

Determining the diet composition of herbivores on rangelands is time consuming (Holechek *et al.*, 1982). MIAMH gives an overview of the diet spectrum in relation to feed on offer, which can be used for evaluating alternative management practices.

To show the flexibility of the model, a simulated experiment was conducted. The first step was to select which of the modelled parameters varied the most in the actual system. Principal component analysis (PCA) was performed on the four parameters evaluated at the rangeland (Table 2). The first two principal components explained 95% of the total variation of the data. The first was associated with the probability of encounter, R_{ij} ($P < 0.01$). The second was a bipolar principal component associated with crude protein content and lignin content ($P < 0.01$). These two parameters define the quality index, Q_i , in the model (eqn (2)).

The prediction of the composition of the diet selected by goats in the coastal scrub of Baja California was simulated by varying the R_{ij} and Q_i of herbs, and maintaining these two variables as constants for all the other forage species. R_{ij} varied from 0.1 to 0.9 and Q_i from 0.5 to 5. Simulated herb contribution to diet varied from 7.5 to 88.8% (Fig. 4). This response surface shows the flexibility of the model in the range simulated, and the interaction of the two variables for diet prediction. The most sensitive variable is R_{ij} , in agreement with the findings of Genin (1992).

A follow-up to the results of this simulation might be to introduce herb species of different qualities in the rangeland, at different densities. The hypothesis would be that if the model prediction is adequate, the quality of the diet might increase significantly.

MIAMH can provide researchers with a preliminary operational tool

TABLE 2
Principal Component Analysis on the Explanatory Variables

Variable	Eigenvectors			
	PC1	PC2	PC3	PC4
Probability of encounter	0.995863	0.074938	-0.048156	-0.017954
Structural index	0.018451	-0.012254	-0.010220	0.999702
Crude protein	0.079068	0.494026	0.865843	0.001337
Lignin	-0.040803	0.866125	0.497887	0.016459
Cumulative	0.80	0.93	0.99	1.00

PC—Principal component.

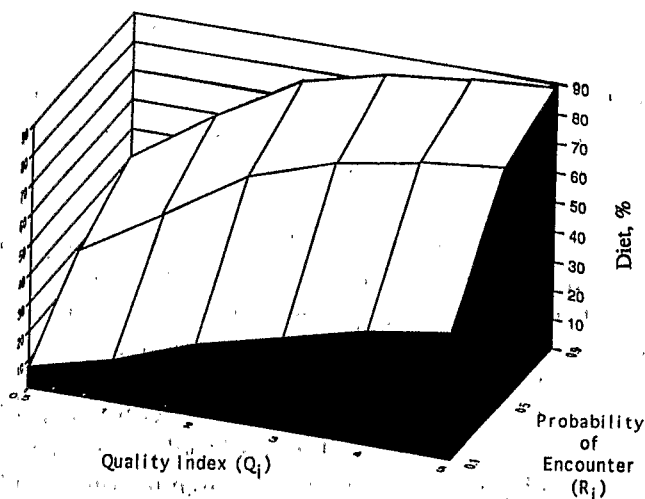


Fig. 4. Response surface of simulated contributions to goat's diet of herbs (in per cent) varying their quality index (Q_i) and their probability of encounter (R_j).

for determining the diet selection process of large herbivores. A second important application is that it can be coupled to other animal production models where diet selection is an input (e.g. Arnold, *et al.*, 1977; Orsini, 1990; Cañas *et al.*, 1991). The integration of these two types of models may allow prediction of range animal production parameters from the knowledge of only the structure and quality of forages on offer in the rangeland, and the animal type foraging. In contrast, using the models separately requires that the users of MIAMH must determine in the field animal production parameters, and those using management models must measure diet selection.

ACKNOWLEDGEMENTS

This paper was much improved by helpful comments of the ecodevelopment unit staff of INRA, Avignon, and an anonymous referee. The authors thank Robert A. Washington for reviewing the text.

REFERENCES

- Arnold, G. W. (1985). Ingestive behaviour. In *Ethology of Farm Animals*, ed. A. J. Fraser. Elsevier, Amsterdam, pp. 183–200.
- Arnold, G. W. & Campbell, N. A. (1972). A model of a lay farming system with particular reference to a sub-model for animal production. *Proc. Austr. Soc. Anim. Prod.*, **9**, 23–30.

- Arnold, G. W., Campbell, N. A. & Galbraith, K. A. (1977). Mathematical relationships and computer routines for a model of food intake, liveweight change and wool production in grazing sheep. *Agric. Systems*, **2**, 209–26.
- Belovsky, G. E. (1978). Diet optimization in a generalist herbivore: the moose. *Theor. Pop. Biol.*, **14**, 105–34.
- Belovsky, G. E. (1981). Food plant selection by a generalist herbivore: the moose. *Ecology*, **62**, 1020–30.
- Cañas, R., Aguilar, C. & Edwards, G. (1991). Modelo de simulación de producción ovina para la zona de Puno, Perú. In *Perspectivas de la Investigación para el Altiplano*, ed. L. Arguelles & R. Dario Estrada. ACIDI-CIID-INIAA, Lima, pp. 87–150.
- Cooper, S. M., Owen-Smith, N. & Bryant, J. P. (1988). Foliage acceptability to browsing ruminant in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia (Berlin)*, **75**, 336–42.
- Coughenour, M. B. (1991). Spatial component of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *J. Range Manage.*, **44**, 530–42.
- Crawley, M. J. (1983). *Herbivory: the Dynamics of Animal-Plant Interactions. Studies in Ecology*, Vol. 10, University of California Press, Berkeley, 437 pp.
- Demment, M. W., Laca, E. A. & Greenwood, G. B. (1987). Intake in grazing ruminants: a conceptual framework. *Proc. Feed Intake Symp.* Oklahoma State University, Oklahoma, pp. 208–25.
- Ellis, J. E., Wieñis, J. A., Rodell, C. F. & Anway, J. C. (1976). A conceptual model of diet selection as an ecosystem process. *J. Theor. Biol.*, **60**, 93–108.
- Freer, M., Davidson, J. L., Armstrong, J. S. & Donnely, J. R. (1970). Simulation of grazing systems. *Proc. XI Int. Grassland Congress.* University of Queensland Press, St Lucia, Australia, pp. 913–17.
- Genin, D. (1990). Les choix alimentaires de la chèvre dans le matorral côtier de Basse Californie (Mexique): perspectives pour une approche prédictive de la sélection alimentaire des ruminants sur parcours. Thèse Doct., Univ. Sci. Tech. du Languedoc, Montpellier, 123 pp.
- Genin, D. (1992). MIAMH: un modèle prédictif des choix alimentaires des ruminants sur parcours. In *Proc. 4th Int. Rangeland Congress, Montpellier*, ed. H. N. Le Houerou. CIRAD-CIDARC, Montpellier, pp. 632–5.
- Genin, D. & Badan, A. (1991). Goat herbivory and plant phenology in a mediterranean shrubland of northern Baja California. *J. Arid Environ.*, **21**, 113–21.
- Genin, D. & Pijoan, P. (1993). Seasonality of goat diet and plant acceptabilities in the coastal scrub of Baja California, Mexico. *Small Ruminant Res.*, **10**, 1–11.
- Goodall, D. W. (1969). Simulating the grazing situation. In *Concepts and Models of Biomathematics*, Vol. 1, ed. F. Heinmets. Marcel Dekker, New York, pp. 211–27.
- Hahley, T. A. (1982). The nutritional basis for food selection by ungulates. *J. Range Manage.*, **35**, 146–51.
- Holechek, J. L., Vavra, M. & Pieper, R. D. (1982). Botanical composition determination of range herbivore diets: a review. *J. Range Manage.*, **35**, 309–15.
- Lachaux, M., Meuret, M. & de Simiane, M. (1987). Composition chimique des végétaux ligneux pâturés en région méditerranéenne française: problème posés par l'interprétation des analyses. In *L'Animal, les Friches et la Forêt*.

- II—*La Forêt et l'Élevage en Région Méditerranéenne Française*, ed. B. Hubert. *Fourrages*, no. Hors Série, pp. 231–67.
- Leclerc, B. (1984). Utilisation du maquis corse par des caprins et des ovins. I— Régime alimentaire des caprins. *Acta Oecol., Oecol. Appl.*, **5**, 383–406.
- Le Houerou, H. N. (1980). Fourrages ligneux en Afrique de Nord. In *Les Fourrages Ligneux en Afrique*, ed. H. N. Le Houerou. CIPEA, Addis Ababa, pp. 57–84.
- McKell, C. M. (1989). Shrub palatability. In *The Biology and Utilization of Shrubs*, ed. C. M. McKell. Academic Press, Cambridge, pp. 267–82.
- Maizeret, C. (1988). Stratégies alimentaires des chevreuils: les fondements écologiques d'une diversification de régime. *Acta Oecol., Oecol. Appl.*, **9**, 191–211.
- Meuret, M. (1989). *Feuillages, Fromages et Flux Ingérés*. INRA, Avignon, 229 pp.
- Orsini, J. P. G. (1990). Summer Pack, a user-friendly simulation software for the management of sheep grazing dry pastures or stubbles. *Agric. Systems*, **33**, 361–76.
- Owen-Smith, N. & Novelie, P. (1982). What should a clever ungulate eat? *Am. Nat.*, **119**, 151–78.
- Pfister, J. A. & Maleček, J. C. (1986). Dietary selection by goats and sheep in a deciduous woodland of northeastern Brazil. *J. Range Manage.*, **39**, 24–8.
- Pulliam, H. R. (1975). Diet optimization with nutrient constraints. *Am. Nat.*, **113**, 765–8.
- Rice, R. W., McNeil, M. D., Jenkins, T. G. & Koong, L. J. (1984). A computer simulation model of the herbage/herbivore interface. *Proc. Int. Rangelands Congress*, Australian Academy of Science, Canberra, eds P. J. Joss, P. W. Lynch & O. B. Williams. pp. 415–16.
- Ruyle, G. B. & Dwyer, D. D. (1985). Feeding stations of sheep as an indicator of diminished forage supply. *J. Anim. Sci.*, **61**, 349–53.
- Schoener, T. W. (1971). Theory of feeding strategies. *An. Rev. Ecol. Syst.*, **11**, 369–404.
- Senft, R. L., Rittenhouse, L. R. & Woodmansee, R. G. (1983). The use of regression models to predict spatial patterns of cattle behavior. *J. Range Manage.*, **36**, 553–7.
- Senft, R. L. (1989). Hierarchical foraging models, effects of stocking and landscape composition of simulated resource used by cattle. *Ecol. Modelling*, **46**, 283–303.
- Senft, R. L., Rittenhouse, L. R. & Woodmansee, R. G. (1985). Factors influencing patterns of grazing behavior on shortgrass steppe. *J. Range Manage.*, **38**, 181–7.
- Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E. & Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies. *Bioscience*, **37**, 789–99.
- Sibbald, A. R., Maxwell, T. J. & Eadie, J. (1979). A conceptual approach to the modelling of herbage intake of hill sheep. *Agric. Systems*, **4**, 119–34.
- Staddon, J. E. R. (1983). *Adaptive Behavior and Learning*. Cambridge University Press, New York, 555 pp.
- Stobbs, T. H. (1973). The effect of plant structure on the intake of tropical pasture. I—Variations in the bite size of grazing cattle. *Aust. J. Agric. Res.*, **24**, 809–19.

- Stuth, J. W. (1991). Foraging behavior. In *Grazing Management*, ed. R. K. Heitschmidt & J. W. Stuth. Timber Press, Portland, OR, pp. 65-84.
- Van Dyne, G. M. (1969). Grasslands management, research and training viewed in a system context. Range Sci. Dep. Sci., Series 3. Colorado State Univ., Fort Collins.
- Van Dyne, G. M., Brockington, N. R., Szocs, Z., Duek, J. & Ribic, C. A. (1980). Large herbivore subsystem. In *Grasslands, Systems Analysis and Man*, ed. A. I. Breymer & G. M. Van Dyne. Int. Biol. ProG., 19.
- Van Soest, P. J. (1982). *Nutritional Ecology of the Ruminant*. O & B Books, Corvallis, OR.
- Vangilder, J. D., Torgerson, F. & Porath, W. R. (1982). Factors influencing diet selection by white-tailed deer. *J. Wildl. Manage.*, **46**, 711-18.
- Westoby, M. (1974). An analysis of diet selection by large generalist herbivores. *Am. Nat.*, **108**, 290-304.
- Westoby, M. (1978). What are the biological bases of varied diets? *Am. Nat.*, **112**, 627-31.