CHAIRS' SUMMARY PAPER: Foraging Strategies

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The concept of foraging strategies implies different things to different individuals. For some researchers, the study of foraging strategies is firmly rooted in comparative anatomy: emphasizing the diverse physiological responses to complex selection gradients. For others, the study of foraging strategies focuses on identification of factors that limit or regulate rates of energy or nutrient intake. Yet a third group emphasizes the plasticity of behavioral decision-making as it applies to feeding processes, particularly in the context of identifying selectively advantageous decisions to changing physiological, environmental, and stochastic circumstances facing a given animal. Perhaps not surprising in light of this far-ranging context, our session on foraging strategies offered an eclectic mix of viewpoints and priorities for future research.

The daily rate of energy gain is necessarily composed of the instantaneous feeding rate multiplied by feeding time. There seems to be a common perception that mechanistic factors influencing feeding rates per se have been more frequently studied and are consequently better understood than factors influencing the time devoted to feeding (Illius, this volume; Hodgson et al., this volume). That is not to say that there isn't more to be learned: the intriguing proportionality between bite depth and sward height defies current mechanistic explanations, in that on short swards animals could seemingly ingest entire ramets (Hodgson et al., this volume) suggesting perhaps the need to invoke behavioral processes in understanding even the most mechanical aspects of feeding. Beyond that, the role of digestive constraints on maximum rates of intake, synergistic effects of different forages on digestibility and retention time, and voluntary controls on retention time in the digestive tract have been scarcely considered in mechanistic models of forage intake. Such considerations are particularly critical in evaluating daily food intake in extensive grazing systems, in which forage quality constraints might be expected to play a particularly important regulatory role.

The most common theoretical approach to predicting foraging strategies is based on optimal foraging theory (OFT), identifying state decision variables that maximize energetic returns with a specified state space (Laca and Demment 1996). Two types of behavioral decisions dominate current research activity in grazing systems: diet selection and patch selection. Several of the presentations in our session focused on aspects of diet selection. One prediction of OFT is that the degree of selectivity for highly nutritious diets is positively associated with forage abundance on offer, nicely demonstrated by Wales et al.'s (this volume) study of dairy cows in our session. Numerous studies in our session examined other aspects of dietary preference in mixed swards (Acosta et al., this volume; Cosgrove et al., this volume; Gordon, this volume; Poli et al., this volume), showing tendencies for selection of the most nutritious items, but perhaps more catholic mixtures of diet than would be strictly expected from OFT models. Some of this could arise from spatial segregation of forages, a common feature of grassland cafeteria trials. The perplexing issue of partial preferences for grass/clover swards was a dominant feature of discussion, as it has been in the recent literature (e.g. Newman et al., 1995; Thornley et al., 1995).

In the oral presentations, however, there seemed to be a growing dissatisfaction with optimal diet choice models (Hodgson et al., this volume; Illius, this volume; Provenza et al., this volume). Thorny issues relate to the degree to which constraints are actually constraining (Illius, this volume), the proper way to incorporate digestive constraints in our models (Hodgson et al., this volume), and the potential role of plant toxins and other secondary compounds in shaping feeding preferences and aversions (Provenza et al., this volume). Moreover, current OFT models do not address the diverse dietary experiences, health status, and cultural environment faced by individuals, all of which have well documented effects on diet selection (Provenza et al., this volume). All of this seems to beg for a more individually-based or state-dependent modification of OFT models or even development of new theory that incorporates dynamic tension between competing behavioral drives (Illius, this volume). This highlights two research priorities: more relevant theory and rigorous comparative tests of alternate dietary models. Rejection of OFT can only come about when it is replaced by better theory.

A second dominant theme in our session had to do with behavioral responses to resource spatial heterogeneity. Checkerboard experiments with swards of different heights suggest adaptive spatial preferences for ramets yielding high energetic gains (de Vries et al., this volume; Griffiths et al., this volume), as predicted by optimal patch use models for swards of different maturational stage (Fryxell 1991). Preferential use of intermediate height classes should lead to bimodal or even multimodal distributions of sward heights within a given pasture, well documented by Aiken et al.'s (this volume) grazing trials. Patchiness seemed to have little to do with dietary selection for grass versus clover (Gordon et al., this volume). One technical roadblock to understanding foraging in complex landscapes is simply remote sensing by free-ranging animals beyond visual contact. An exciting step in this direction was offered by Lawrence and Becker's (this volume) horn-mounted vibration detector. Further progress in this field depends to some degree on developing simple means of modelling step-by-step movement patterns by foragers through a complex landscape - an obvious priority for future research (Hodgson et al., this volume).

Our group discussions repeatedly returned to two nagging problems. First, the questions and priorities at the research level don't seem to coincide with the perceived needs and priorities of the extension and commercial user communities. To some degree this is inevitable, of course, because cutting edge research is necessarily a decade ahead of expert systems. It raises a second, potentially deeper, issue. Rather than looking for unambiguous technical advice, perhaps an adaptive management framework is called for, emphasizing controlled experimental comparisons at the practitioner level to assess exciting new research findings.

Our session demonstrated the impressive depth and breadth of current research in foraging strategies in livestock systems. It did little to address comparisons with other organisms, such as wild ungulates, geese, or rodents living in grassland communities. Given the differences in selection regimes experienced by domesticated versus wild animals, comparative experimental foraging studies seems a useful priority for future research.

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