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When Art and Science Meet: Integrating Knowledge of French Herders with Science of Foraging Behavior

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ABSTRACT

Landscapes are complex creative systems that continually transform due to ever-changing relationships among environments and organisms including human beings. During the past half-century, those who study these relationships and those who manage them have become increasingly isolated from one another in their attempts to understand and manage landscapes. As we have come to rely on experimental science to understand principles, we have diminished the importance of experiential knowledge in understanding and implementing practices. In this paper, we discuss convergence of the knowledge of herders from Southeastern France with the science of foraging behavior. We review insights of researchers gained through interviews with herders, surveys, and in situ recordings of the foraging behavior of closely herded sheep and goats. Though years of hands-on experience, herders have come to understand processes involved in food and habitat selection. Using a conceptual model of four steps, which represent four intertwined processes for a given herder-herd-fodder resource, we describe how herders 1) teach their animals to use the full range of forages, 2) train the herd to respect the boundaries of grazing areas, 3) modulate what they call the "temporary palatability scoring" of forages, and 4) establish daily grazing circuits to stimulate appetite and intake through meal sequencing. This knowledge is also valuable when the objective is to boost appetite for particular forages, such as coarse grasses, scrub, and invasive species. The practices of herders are consistent with scientific studies that show the importance of plant biodiversity for enabling animals to select nutritious diets and the significance of animal learning and culture on nutrition, production, and health. We conclude by highlighting implications for furthering the exchange between herders and scientists and by providing implications for managing grazing on pastures and rangelands, with or without shepherds and dogs, and targeting grazing on particular plants and habitats.

When Art and Science Meet

During the past 3 centuries, we've come to rely on experimental science to understand processes of nature (Capra, 1982). In so doing we've diminished the importance of experiential knowledge that comes to people's brains through their hands ("know that" vs. "know-how") (Kauffman, 2000). In accenting parts (cognitive, rational, analytical) over wholes (noncognitive, intuitive, synthetic), we've created challenges that arise from our inability to fully appreciate the interrelated and dynamic nature of landscapes in time and space. However, different ways of knowing can support and enrich one another and lend insights into processes: in the case of grazing, the complementarity between the hands-on acquisition of knowledge by managers and the experimental knowledge of scientists. Integrating science and art provides insights into ways to manage interactions among soil, plants, herbivores, and humans.

Landscapes are complex, creative ecological and social systems that endlessly emerge, transform, and disappear due to ever-changing relationships among organisms and biophysical environments (Provenza et al., 2013). All organisms, not just *Homo sapiens*, actively participate in creating environments—they aren't just passively adapting to them. In science, creativity is manifest as a quest to understand principles and processes of transformation. In practice, land managers best evolve within prevailing ecological, economic, and social conditions by linking understanding of principles and processes with the flexibility to respond to change.

Neither scientists nor managers are good at anticipating, predicting, or controlling change because we don't know enough to foresee the consequences of our actions and because environments often respond to our actions in ways no one expects. If we lack

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flexibility, we can't evolve with the changes we help create (Senge, 1994). At our best, we interact with biophysical environments and adjust our behavior on the basis of any feedback we can gain, a process that in both science and practice involves setting goals; devising plans that embrace change; monitoring ecological, economic, and social conditions; and continually adjusting and re-creating. Although both researchers and managers attempt to appreciate and transform within a web of ever-evolving relationships, we've become increasingly isolated in our endeavors (Hubert et al., 2014). In partnership, scientists and managers can better understand principles and processes and link them with the decision-making practices: preemptive and creative management within the framework of distinctively personal goals. In the process, researchers and managers can become allied and linked, from the ground up, with the challenges and opportunities we face as social, economic, ecological, and political landscapes transform.

In this paper, we explore the interface between art and science by integrating the experiential knowledge of talented French herders with the science of foraging behavior. We highlight the kind of innovation that is possible if people create relationships with landscapes, which the science of foraging behavior underscores: Plants and animals aren't machines and genes aren't destiny. Rather, we are all actively participating in creating the locales we inhabit. Unfortunately, our methods and metaphors both in science and practice often reinforce rigid ways of thinking and behaving, reflected in our use of rather inflexible terms such as "adaptation" (Provenza et al., 2013). In this paper, we stress fluidity as opposed to rigidity; intimate human contact with plants, animals, and landscapes as opposed to fences to manage grazing; ever-emerging relationships among genes, organisms, and environments as opposed to genetics and breeds; animals as individuals, not anonymous members of species; and individuals as members of social groups with a structure and integrity to be carefully considered in grazing.

Recreating Relationships among Human Beings, Livestock, and Landscapes

Historically in North America, livestock roamed about landscapes and they were fenced out of areas such as family vegetable gardens and croplands. Over time, livestock owners began to fence grasslands to keep other folks' livestock out. Most recently, fences have been used in attempts to disperse animals across landscapes to obtain moderate use of key plant species and areas (Provenza, 2003a). Yet preferred areas were still being degraded, especially riparian areas, while uplands were underused, which led to reductions in numbers on federally administered lands. In recent times in France, low-lying areas at the bases of mountains were often underused by livestock when fences were promoted to reduce the time and cost of herding, a practice that emerged early in the Neolithic, around 6 000 B.P. (Delhon et al., 2008).

All of these issues are behavioral. Animals use plant communities differentially, and their preferences are affected by how they learn to use the heterogeneity of landscapes to obtain forage, water, and cover (Teague et al., 2013). Patterns of use are influenced by topography, vegetation patchiness, shade, wind, mineral licks, intraspecific and interspecific social relationships among herbivores, and interactions with predators including insects. These factors interact to increase vegetation heterogeneity as the size of a fenced pasture increases: They can cause heavy, repeated impacts on preferred areas, while other areas receive light or no utilization.

Livestock foraging on rangelands select meals from grasses, forbs, shrubs, lianas, and trees. At any time or place, some species are more or less nutritious while others are more or less toxic. Individual plants within a species can be either nutritious or toxic depending on the time of the day, week, and season; on the resources available in the environment where the plant is growing; and on the age and past experiences of the plant with grazing. Herbivores may sample 50 or more foods in a day, though 3 to 5 items typically make up the bulk of a meal. What they choose changes from meal to meal daily, seasonally, and annually.

These complexities bring into question efforts to construct food tables and rank food preferences, yet for centuries researchers attempted to do so on the basis of digestibilities and metabolizabilities of primary compounds—energy, protein, and minerals—as they affect food intake and animal production (see historical synthesis by Johnston, 1843). Due to the effort required, most research was done in confinement with easily harvested foods, often fed singly or rarely in combination. Although interactions among foods were acknowledged, their contributions to the diet were assessed by adding values for each food. This may work when foods are fed singly or in simple combinations, but it is not valid on rangelands where herbivores eat many different forages in a meal. Nor did scientists appreciate the roles of secondary compounds, the over 8 000 phenolics, 25 000 terpenes, and 12 000 alkaloids recorded in various plant species to date. The thousands of compounds consumed in a meal influence food intake, nutritive, and medicinal values in ways scientists are just beginning to appreciate (Provenza et al., 2015).

As we have come to better appreciate these complexities, livestock nutritionists and wildlife ecologists questioned the abilities of herbivores to select a diet from a diverse and ever-changing array of plants. They asked, rightly so, how can animals relate specific foods with their nutritional or toxicological consequences when they eat such complex and ever-changing mixtures of plants? Although most experts considered this question overwhelming, in the past 40 yr researchers have made advances in understanding how herbivores learn which foods to eat, how to mix various foods in their diets, and which places to forage. In the process, we have moved away from rigid notions of herbivores as grazers (cattle), mixed-feeders (sheep), and browsers (goats) to a better understanding of how herbivores can learn to become any of these depending on context: Grazers can live nicely on diets of shrubs and browsers can survive primarily on grass if they learn to do so (Provenza, 1995b; Provenza et al., 2003). Experiences in utero and early in life change form, function, and behavior of herbivores. This leads to the hypothesis that different ways of managing grazing change the abilities of livestock to forage in different ways—some encourage animals to eat a variety of foods and forage in a variety of places, while others do not (Provenza, 2003a,b). That, in turn, raises a question: By focusing management on "key areas" and "key species" of plants, might we inadvertently train animals to "eat the best and leave the rest" rather than to "mix the best with the rest," thereby creating herbivore cultures that behave in ways counter to what we desire?

One of the most sophisticated ways to encourage animals to eat a variety of foods and forage in a variety of places involves close herding using experiential understanding of relationships among soil, plants, herbivores, herders, and their herding dogs. While herding may seem old-fashioned, it unites two areas of growing interest and competence in many parts of the world: low-stress techniques for moving and placing animals (Smith, 1998; Cote, 2004; Hibbard, 2012) and management-intensive grazing (Savory, 1983; Gerrish, 2004). Managers are learning to move and place livestock in ways that minimize stress to animals and herders. They are also using management-intensive grazing, moving livestock at least once, if not several times, daily. That is creating a mind-frame that can accept moving and placing animals regularly throughout the day as part of grazing circuits to enhance health of animals and land. Even 10 yr ago, these ideas would have been shocking to land managers in the United States, but given interest in more intensive management and the many nowrecognized benefits of properly managed grazing for soil, plants, herbivores, and people, they are no longer outrageous. Activities such as herding—described as "old fashioned" — come back "in vogue" as human needs and values change.

Animal Scientists Working with Herders

Anthropologists, ethnologists, geographers, and specialists in livestock systems have studied pastoral societies and herders, mostly nomads living in arid and semiarid environments. Most studies dealt with the complexity of pastoralism in relation to social and biophysical dimensions of the environment with cattle in arid and semiarid environments of Africa and reindeer in the Arctic (Evans-Pritchard, 1939; Dyson-Hudson and Dyson-Hudson, 1980; Niamir-Fuller, 1998). Nearly 20 yr ago, scientists became interested in Traditional Ecological Knowledge (TEK) (Berkes et al., 2000). Inspired by studies of anthropologist Levi-Strauss (1962), they attempted to mix social science and biology to understand indigenous knowledge and values attributed to the environments and resident natural resources. With regard to pastoralists, studies dealt with how herding systems respond to conflicts and changes in land-use policy and climate. Their approaches centered on community-based management, livelihoods, human-animal relationships, resource scarcity and uncertainty, and on perceptions of pastoralists of animal performance and rangeland vegetation for forage and medicine (e.g., Copolillo, 2000; Oba and Kaitira, 2006; Dwyer and Istomin, 2008; Wurzinger et al., 2008; Krätli and Schareika, 2010; Retta et al., 2013; Landau et al., 2014; Molnar, 2014).

Now in France, as in many industrialized countries, herders no longer belong to a pastoral society with TEK. Only herders from some valleys in the Western Pyrenees and Corsica still have a traditional, but ever-evolving, herding culture transmitted orally over generations. In other regions, the absence of a community-based culture is due to rapid changes in landscapes, plant communities, herd size, expected levels of animal production, food market globalization, and environmental policies. Thus French herders had to become imaginative and creative while building, most of the time in a quite solitary way, their individual wealth of experiential knowledge (Baumont, 2014), such that TEK approaches and paradigms are not applicable.

French Context for Herding on Rangeland Today

In the European sense, rangelands comprise all parts of land not subjected to either agricultural operations or forest plantation and management. These rugged terrains were used for centuries, mostly to feed domestic herbivores through herding and to produce manure for local croplands (Hubert et al., 2014). In the 20th century, high mountain grazing places were still used in summer by long-range transhumant sheep farmers; all the other rangelands, which served no purpose in the course of the agricultural "modernization," were left fallow and became progressively covered with scrubs and trees. As a consequence, wildfires annually devastated hundreds of hectares within a few hours in southern France and forest managers and local policy makers began to promote reintroducing grazing on scrubby rangelands (Hubert et al., 2008). In the early 1990s, proper rangeland grazing was also promoted by the European Union as an ecological service to help conserve and restore biodiversity and protect habitats for fauna and flora (Hubert et al., 2014). Considering that most rangelands in France are also public lands used for multiple purposes such as hiking and hunting, and can hardly be fenced to manage grazing, herding recently regained great interest for land managers.

Most French sheep farmers hire salaried herders, especially farmers who are grouping their animals in large collective flocks for winter and summer long-range transhumance (Legeard et al., 2014). Some goat and sheep farmers herd their own animals to reduce food costs and facilitate temporary access to privately owned lands. As a result, France has a robust demand for skilled herders. That has caused France to create and financially support five herding schools, each with programs for trainees mostly from urban backgrounds (Jallet et al., 2014).

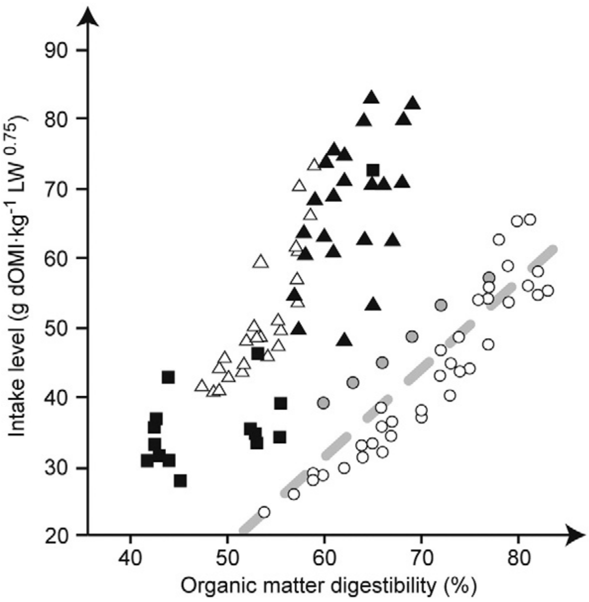

Fig. 1. Intake by goats (black triangles) and sheep (black squares) eating mixed diets on rangeland or goats (white triangles) fed fresh oak foliage in specially designed digestibility crates. Each data point represents the average daily response of an individual for 5 to 12 d. With equivalent digestibility of organic matter, we recorded double the intake reported in the literature for sheep fed in crates with cultivated fresh grass (white circles) or fresh lucerne (gray circles). Intake levels are expressed as digestible organic matter ingested (dOMI) kg^{-1} LiveWeight$^{0.75}$ of the animal (after Jarrige, 1988; Meuret, 1989; Baumont et al., 1999; Agreil and Meuret, 2004). The reference linear model on the right (thick gray dotted line) is based on data from Morley (1981) and Van Soest (1994).

Why and How Animal Scientists Worked with Herders

When we began studying the behavior of closely herded sheep and goats on scrubby rangelands from Southeastern France, we were perplexed to see such high levels of forage intake. For each rangeland and grazing condition, we recorded daily intakes much higher than those for animals fed forages of similar nutritive value in laboratory crates (Fig. 1). Assuming equal nutritive value of the diet, animals were eating twice as much as expected (thick gray dotted line in Fig. 1). Given diets of medium nutritive value (50% to 70% digestible organic matter), intake of digestible organic matter was often higher for sheep at pasture compared with sheep in laboratory crates, even when fed excellent forage such as fresh lucerne (*Medicago sativa* L.). When we published the results, nutritionists were surprised and suspected erroneous measurements. To see if this was so, we fed dairy goats fresh oak foliage (*Quercus ilex* L. or *Q. pubescens* Willd.), in specially designed crates, with similar results (white triangles in Fig. 1) (Meuret, 1988). We also confirmed that the same goats, fed only lucerne hay, had intakes as expected from animal nutritional references (Meuret and Giger-Reverdin, 1990).

The data in Fig. 1 were obtained under two regimens: 1) animals in laboratory crates, which mimic feeding at the trough (white circles), where animals are offered a single, homogenous forage for many days to assess nutritional value, and 2) animals herded on rangeland (black triangles), grazed on rangeland with a moveable fencing device controlled by a herder (black squares), or fed oak foliage (white triangles) in specially designed digestibility crates

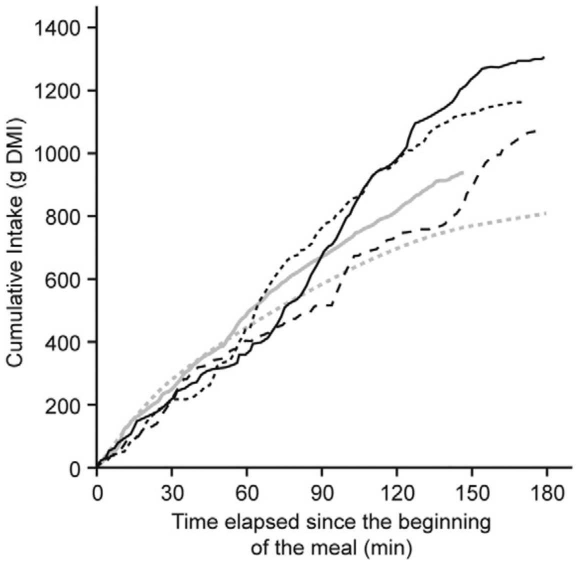

Fig. 2. Cumulative intake of dry matter (DMI) in the course of three evening meals recorded in summer for a dairy goat being herded on woody rangeland (after Meuret, 1989). The slope and regularity of the curves reflect the animal's motivation to eat the forages. For comparison, there is also a curve for the intake of fresh grass eaten out of a trough by a dry-ewe (gray dotted curve in the background, after Baumont, 1989) and a curve for a dry-ewe having her first meal when the flock entered a newly fenced rangeland pasture (solid gray curve in the middle, after Agreil and Meuret, 2004).

where animals were offered fresh leafy branches, constantly renewed during meals to mimic a grazing situation; with oak, one species was offered for 2 wk, but the polymorphism of oak foliage positively impacted intake (Meuret, 1988). On rangeland, the digestible organic matter of the wide range of plant species and parts herbivores ingest varies from 30% to 90% daily (Meuret, 1989; Agreil et al., 2006). Averaging digestibility values of such diverse forages masks the stimulatory effect of variety on appetite (Meuret and Bruchou, 1994).

Even after these trials, it was still unclear why animals ate so much forage on rangeland. To gain further insight, we examined cumulative intake within a meal, which reflects foraging motivation. Our calculations showed excellent motivation when goats were closely herded on rangeland (Fig. 2). Intake rates (g dry matter min^{-1}) at the beginning of a meal were often as high as those when sheep are placed on fresh rangeland pasture (Agreil and Meuret, 2004) or provided first-rate grass forage in troughs (Baumont, 1989). The "constants of deceleration" for the curves, as a function of satiation, were low (Meuret, 1989). Thus in three evening meals in Fig. 2, the herder was successful in getting goats to eat from 1.1 to 1.3 kg of dry matter per meal, which is high, especially in only 3 h foraging just before nightfall. These meal curves (kinetics) have quite different shapes from those usually obtained with animals fed in troughs or derived from animals eating their first meal on a newly fenced rangeland pasture, where simple exponential models accurately fit cumulative intakes during meals (gray curves in Fig. 2). With herding, after a phase of partial satiation, an animal quickly regains a hearty appetite during the next phase of the meal. How does herding prompt the frequent renewal of appetite within a meal? To answer this question, we began to work with experienced herders.

Mixing Methods to Understand and Model Herders' Knowledge and Practices

To understand and model herding practices, we began working closely with shepherds and goat herders while simultaneously

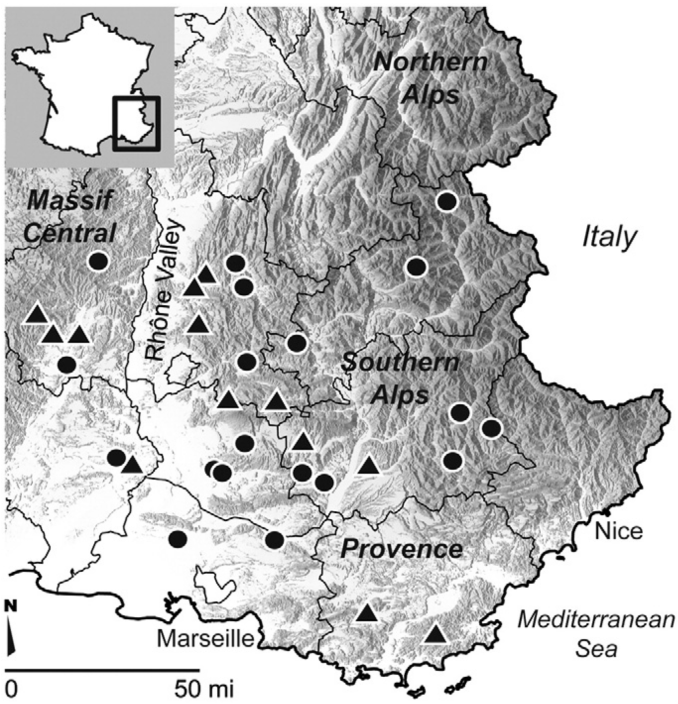

Fig. 3. Location of 31 herders we interviewed in Southeastern France. Goat herders, black triangles; Shepherds, black circles (Topographic data source: NASA/NGA/USGS public domain).

using three approaches adapted from animal behavior science, landscape ecology, and ethnology. We interviewed 31 herders dispersed throughout Southeastern France (Fig. 3). We recorded forage intake with herded animals in situ with a subsample of seven herders that were most interested and available.

Our first method was the semistructured interview (Kauffman, 1996; Yin, 2003). Dialogues were informal and we accepted any response to our questions, which focused on personal herding experience. We first selected two herders who had exchanged part of their experience with researchers (Meuret et al., 1985; Landais and Deffontaines, 1989). They referred us to colleagues likely to be interested in our work, and they, in turn, referred us to yet others. We first chose cheese-producing goat herders because they had a reliable and easy-to-record indicator of foraging success: twice-a-day variation in milk and cheese production, which reflected meal quality. We also interviewed lamb-producing sheep farmers who herd their own flocks. Herders were 24 to 57 yr old, all with experience herding in many places. All herders had worked for at least 3 consecutive years on the same place with the same herd and some had 15 yr of experience on the same place. After the interviews, we circulated their various perceptions and statements without citing individual sources and we prepared discussions among herders, which resulted in clarification of some statements. Finally, we asked 10 highly motivated herders to co-conceive with us a model of grazing circuits (MENU, see later).

Our second method was to ask a subsample of seven particularly motivated herders to take notes in situ as they conducted daily grazing circuits, including the times and sequences in which various locations were grazed, and the reasons for their herding actions. Herders recorded these data on a blank base map (1:1 500 or 1:3 000, depending on the grazing area extent) while herding along the grazing circuit. We analyzed the daily recordings at the scale of each grazing location using GIS mapping software (Miellet and Meuret, 1993).

Our third method involved making simultaneous measurements in situ during a time of year (e.g., late spring or summer, depending on the yearly grazing schedule of the herd) when the entire intake at pasture was under a herder's control. Measures were carried out by recordings of 1) the type and condition of grazed areas, 2) the pattern of activity of the herder and the herd in grazing circuits, and 3) the instantaneous intake rate of a constantly monitored animal. We used the direct and continuous bite monitoring method we initially developed to record individual intake in herded dairy goats on rangelands (Meuret et al., 1985; reviewed in Bonnet et al., 2015 with developments for other ruminant species and grazing conditions). The centerpiece of our method is the conception of a "bite coding grid" that much improves the estimation of bite masses, structures, and quality. The other characteristic of the method is the "mutual familiarization procedure" between animals and observer, which results in the observer being able to move around the monitored individual at a distance of 0.5 to 2 m without any detectable changes in individual and group behavior.

Integrating Knowledge of Herders and Scientists

In what follows, we describe how the knowledge of experienced French herders and the studies of scientists converge and support one another in principle and practice. Herders' observations and practices validated studies that show the advantages of plant biodiversity for enabling animals to select nutritious diets that enhance performance; they corroborate studies of the past 4 decades that show the importance of animal learning and culture on nutrition, production, and health; and they validated studies of plant complementarities and encouraged studies of foraging sequences. The integration of art (herders' know-how) and science (scientists' know-that) would not be possible without another kind of scientific approach: exploratory understanding and system modeling of herders' experiential knowledge and practices through collaborative research between herders and scientists.

As with other grazing techniques, herders must address three challenges: 1) ensure consistent foraging by the animals that fits production objectives of the farmer; 2) fully use the diversity of plants available by not allowing animals to focus only on preferred forages and locations; and 3) contribute to the ongoing renewal of forage resources. To accomplish these objectives, experienced herders plan and manage four steps of action over scales of time that range from minutes to days to years (Fig. 4). These steps represent four intertwined processes for a given herder-herd-fodder resource relationship.

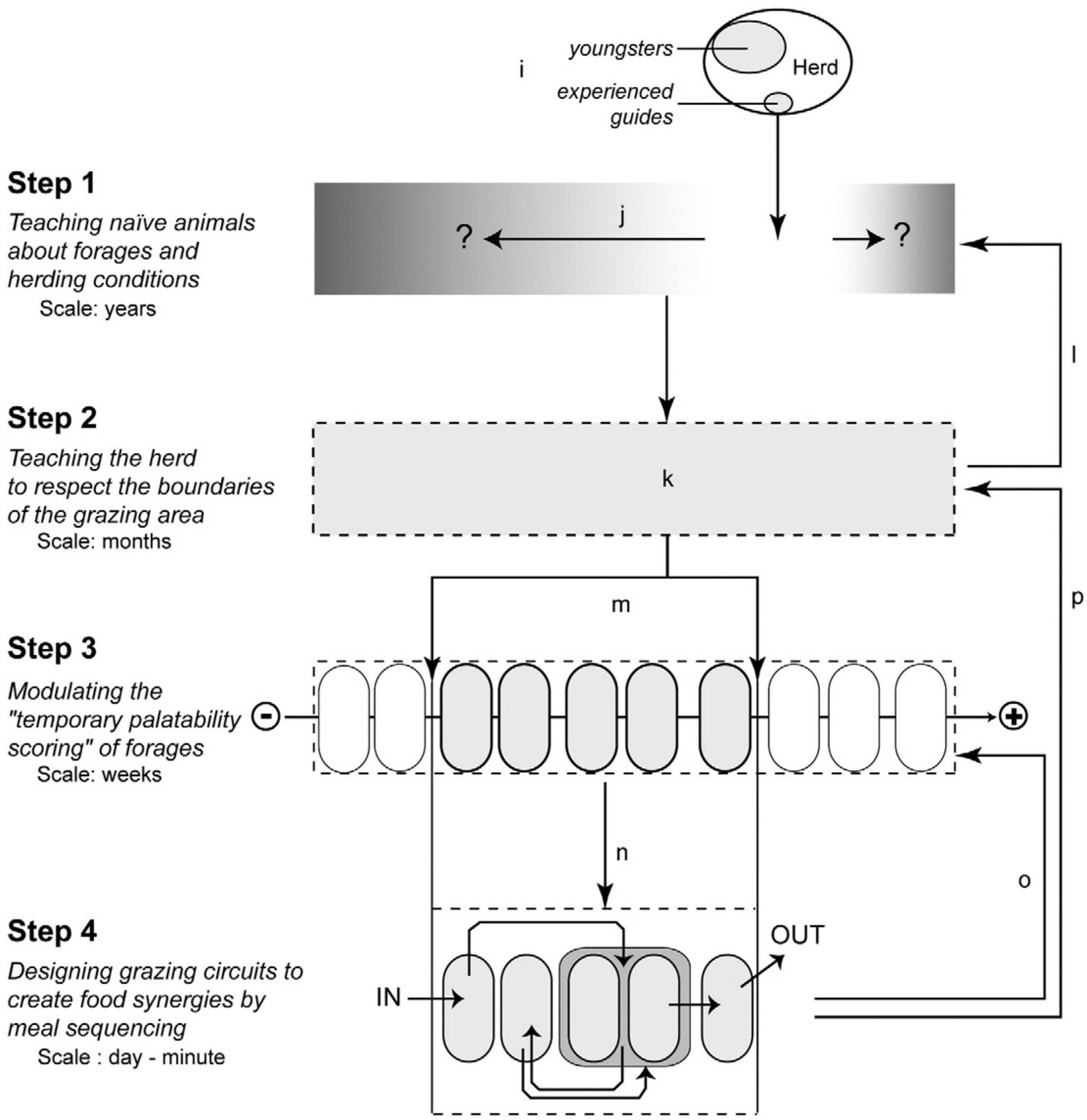

Fig. 4. Conceptual model of the four steps that represent the four intertwined processes for a given herder-herd-fodder resource relationship. These steps, briefly described in the figure, correspond with the letters 'i' to 'p' that are discussed in more detail in the text.

Step 1: Teaching Naïve Animals About Forages and Herding Conditions

This step involves developing relationships among the flock, the herder, and the dog(s) to make the movements of the herd more predictable, including the pace of foraging and forage choices. Herders want to minimize uncertainty in the herd-dog-herder relationship for a given season and grazing location, which in turn improves the herd's ability to predict and interpret the herder's actions, assuming the herder and the dog(s) adopt unambiguous behaviors.

Herding involves managing at three scales: the herd, subgroups, and individuals. A herder seeks to develop a relationship of trust with the entire herd, and he trains herding dogs with the herd in mind. Within the herd, subgroup behavior often prevails over individual behavior and a herder must account for this collective behavior when modulating the behavior of the herd. At the subgroup level, a herder must identify behavioral issues likely to arise in winter or summer transhumance, when he is entrusted with different groups of animals coming from several farms having different rearing practices. In this case, the effects of breed, size, agility, and most of all different foraging experiences help herders distinguish among behaviors of different subgroups. Finally, at the individual level, the herder must identify health issues that affect walking abilities; body condition; milk production; personalities that can positively or negatively impact behavior of the herd or subgroups; and preferences for atypical foods.

For management purposes, most shepherds, and all goat herders, focus their attention on inexperienced animals, mostly the youngest animals, and the "experienced guides" who "understand quickly what is expected and induce others to follow" (see "i" on top of Fig. 4). Guides are kept, even if their performance is average, for their positive influence on the herd. They are fitted with a bell, which reinforces the herd's cohesion, especially in fog, shrubby, or wooded areas. By managing these two groups, the herder is assured of a minimum amount of trouble from the rest of the individuals, often referred to as the "nameless ones" by the herders.

For herders, it is critical to enable animals to learn about grazing conditions and forages they have not previously encountered (see "j" in Fig. 4). Currently in France, many herders are entrusted with flocks of sheep naïve to rangeland grazing. Their lack of experience comes from the intensification of farming conditions in which sheep graze only high-quality cultivated meadows in spring and fall. Sheep farmers want to limit feeding costs, unaware that their sheep fail to recognize much rangeland forage as edible. Naïve sheep also ignore herding dogs. Groups of animals are moved from one pasture to another with quads and trucks rather than with dogs. When released from the transhumance truck, they are confused and can become out of control. They spend most of their time searching for young grasses that resemble foods they know. Without constant pushing by the herder, they are reluctant to become part of a herd of experienced animals. This is true for all breeds, even gregarious breeds such as Merinos.

Training involves three steps: 1) Upon arrival at the grazing allotment, a herder places the sheep for 2 to 3 d in a small fenced pasture (about 1 ha) with familiar, palatable forages. This is helpful to make observations about how the sheep behave in the new environment and to let the sheep meet the dogs, as the herders say, "to check their initial state of mind." 2) The herder then mixes naïve with experienced sheep and herds the whole group within a specific "schooling area," mostly composed of grass, but surrounded by mixed vegetation patches with edible forages as yet unknown to naïve sheep. Once they are partly satiated with grass, the naïve sheep see the experienced sheep grazing and browsing other forages and they become curious to smell and taste them. Learning is enhanced if naïve sheep have reached a state of partial satiation with known grasses and if they can imitate the feeding diversification of experienced sheep. 3) Progressively, the herder leads the sheep on larger daily grazing circuits with longer phases on familiar forages, sequenced with shorter ones on patches with novel forages. This step takes place over weeks and is partially recreated annually. The procedure, which is the same with subadult females, lambs, and kids, is accelerated in suckling animals due to the imitation behavior of a young animal for its mother and other inspiring adults.

Studies of foraging behavior show that herbivores develop habits that can prevent or encourage use of particular foods and habitats (Provenza and Cincotta, 1993). As a result of such learned habits, adult animals introduced to unfamiliar forages and habitats often spend inordinate amounts of time searching for familiar foods (Gluesing and Balph, 1980) and they are often less productive than animals experienced with the foods and environments (Provenza, 2003b). Through close herding, animals can learn new patterns of behavior as a herder trains inexperienced animals where to go and what to eat with the help of experienced "guides" or social models known to play key roles in the learning of food preferences. While "old herbivores" can learn new foraging behaviors, young animals learn more quickly as they are relatively more impressionable in form, function, and behavior (Provenza, 2003b).

Preferences begin in utero through exposure to flavors in the mother's diet (Simitzis et al., 2008). Flavors of onion and garlic, for instance, are transferred in utero and in milk, preparing young animals to eat onion and garlic (Nolte et al., 1992; Nolte and Provenza, 1992a,b). After birth, young animals learn what and what not to eat and where and where not to go from their mothers (e.g., sheep—Hunter and Milner, 1963; Mirza and Provenza, 1990, 1992; Thorhallsdottir et al., 1990; goats—Biquand and Biquand-Guyot, 1992; Howery et al., 1998; cattle—Wiedmeier et al., 2002, 2012). They also learn the motor skills required to harvest different growth forms—grasses, forbs, and shrubs (Flores et al., 1989a,b,c; Ortega Reyes and Provenza, 1993a,b). While mother is vital, other adults and peers also influence food and habitat selection (Thorhallsdottir et al., 1990; Howery et al., 1996, 1998; Ralphs and Provenza, 1999). These findings are consistent with research that shows the importance of learning early in life in the development of food and habitat preferences of insects, fish, birds, and mammals (Davis and Stamps, 2004).

As herders' experiences suggest, livestock learn quickly, they remember for years, and what they learn has a life-long influence on their behavior. Lambs exposed to a novel food with their mothers for 1 h day^{-1} for 5 d at 6 wk of age remember that food when it is offered 3 yr later; compared with lambs exposed to wheat grain alone or not exposed at all, lambs exposed with their mothers eat nearly 10 times more wheat (Green et al., 1984). Likewise, calves exposed with their mothers to ammoniated straw for 2 mo remembered straw 5 yr later—with no intervening experience—and throughout a 3-yr study, cows that ate straw early in life maintained higher body weight and condition and they had shorter postpartum intervals than cows that lacked exposure to straw early in life (Wiedmeier et al., 2002). Cross-fostering studies show that goats from different breeds, one breed which prefers high-tannin browse and the other which does not, eat more (or less) high-tannin browse if they were raised from birth by a foster mother that eats (or does not eat) high-tannin browse (Glasser et al., 2009).

Herders thus have good reason to be concerned about the origins of animals entrusted to them by farmers, but as with many livestock farmers, they are unaware that acquisition of experiences starts in utero (Provenza and Balph, 1990; Provenza, 1995b, 2003a,b). Nor do they realize that changes in foraging behavior are underlain by changes in form and function, which facilitate the behavior. Rumen papillae development and performance are enhanced when lambs fed a high-concentrate diet with mother early in life eat a high-concentrate diet in drylot later in life (Ortega Reyes et al., 1992). Compared with goats naïve to blackbrush (*Coleogyne ramosissima* Torr.), goats reared from 1 to 4 mo of age with their mothers on blackbrush-dominated range ate much more blackbrush during month-long trials at 4 mo (250% more) and 13 mo (30% more) of age; experienced goats also ate 30% more blackbrush than inexperienced goats when they could choose between blackbrush and alfalfa pellets at any level of alfalfa pellet availability (Distel and Provenza, 1991). Compared with goats reared on a high-quality diet, goats reared on blackbrush developed much larger rumens, which facilitated living on a poor-quality diet. Likewise, relative to lambs reared on more digestible, nitrogen-rich forages, lambs reared on poorly digestible forages low in nitrogen eat more of those forages and they digest them better in part because they recycle nitrogen better (Distel et al., 1994, 1996). Compared with lambs born from mothers who foraged on grass pasture during pregnancy, lambs previously exposed in utero by their mothers to a saltbush diet (*Atriplex* spp.) handle a salt load better, excrete salt more rapidly, drink less water, maintain higher intake when eating saltbush, and grow faster (Chadwick et al., 2009a,b,c). Calves exposed in utero or early in life to high-fiber diets eat more high-fiber foods and digest high-fiber diets better than calves exposed to low-fiber diets (Wiedmeier et al., 2002, 2012). Consistent with the importance of learning, heritability of dry matter intake and digestibility of low-quality forages is only 20% (Wiedmeier et al., 1995).

Step 2: Teaching the Herd to Respect the Boundaries of the Grazing Area

Once animals are knowledgeable about forages, the next step for herders is to teach the herd which foraging locations are available in a certain period of the grazing season (see "k" in Fig. 4). Herders whose designated areas are not delimited by impassable obstacles, such as cliffs, rivers, and fences, do not enjoy acting as a "movable fence." They prefer to be a guide who relies on positive reinforcement from taking the herd to places they want to be, rather than negative reinforcement or punishment to enforce boundaries, so they rely on the herding dogs to condition the herd to observe and respect boundaries. This training occurs the first time an area of land is used and at the beginning of each season, as herders say "to refresh the herd's memory." Herders appreciate that sheep and goats have excellent memories, and they can rely on the persistence of memory for habitats for 2 to 3 yr. That's why they ask breeders to entrust them each year with a majority of experienced animals: "It's much easier for me to work, as most of the herd already respects the boundaries of the grazing place!"

Enforcing boundaries consists of allowing animals to move toward a given borderline, such as a mountain crest, a forest edge, or a large track, and then firmly preventing them from crossing. For the first few days, the herder places himself in front of the flock. When the herd approaches a boundary, the herder shouts a specific command (e.g., "Hooo!"), which the animals already understand, and he uses the dog(s) to mark the boundary. As a result of these behaviors, the herd turns around. In the days that follow, when grazing the same area, the herder simply has to stay visible to most of the sheep and to have a dog sit calmly and quietly along the boundary. If the herd attempts to cross the boundary, the herder may cry out as on the first day but this time he remains behind the herd. After training, the herd turns around by itself at the boundary. A herder must pay close attention to subgroup movements near the boundary, especially when forages on the other side of the boundary are becoming more attractive. While enforcing boundaries, a herder also enables a herd to discover the range of forages on offer such that this step enlarges upon and reinforces teaching begun in step 1 (see "l" in Fig. 4).

For most people, it is stunning to see a flock of 1 000 to 2 000 sheep make a smooth U-turn, with the herder and his dogs in the distance, when the flock reaches a grassy mountain crest that is the boundary of its grazing place—the flock has learned and remembers the boundary. The same occurs when a goat herd, walking in a line along a trail, suddenly stops because a rock that fell from the hill the previous night is now on the path. In both cases, people are astonished with learning and memory, caution and curiosity, in animals. Experienced herders know well these capabilities, and as one of them put it, "When I lose myself in deep woods, I often rely on my goats, and dogs, to bring us home safely."

Spatial memory, which has been studied for 50 yr in rats, apes, pigeons, and elephants, has been categorized as "reference" (long-term) and "working" (short-term) memory (Honig et al., 1978; Olton, 1978). The former is the maplike depiction of an area and the amount and quality of food at various locations; the latter is used to recall locations visited during a trial, as in arenas with cattle using shrubs as visual cues (Bailey et al., 1989), and with cattle or sheep with no visual cues other than distal landmarks to orient (Laca, 1998; Dumont and Petit, 1998). In rather small areas (50 × 50 m for steers in Laca's experiment) and simple environments with a few foods, researchers concluded that herbivores can remember the locations and availabilities of food (reference memory) for at least 20 d and they can remember which locations have been recently depleted of food (working memory) for at least 8 hr (Bailey, 1996). Animals remember the locations of preferred foods more readily when they are aggregated than when they are dispersed (Bailey et al., 1998). On rangelands, reference memory is important when patches of food are numerous, distant, diverse, and intricate or when topography, vegetation structure, and strong wind impedes the use of visual and olfactory cues. Animals probably do not remember the locations of every plant in a grazing area of 1 000 ha, nor do they know when availabilities and qualities of forages change rapidly due to local impacts of other domestic and wild herbivores. They learn and remember "focal points of attraction" including locations of water, various habitat types and the mixtures of forages they contain, as well as resting areas. Animals learn about habitat types, the locations of food patches in those habitats, and forages they are likely to find in a food patch at a given time (Senft et al., 1987). Research thus supports the contention of herders that livestock learn the kinds of forages in different habitats, and they remember from year to year when different forages are likely to be edible.

Experiences of herders add interesting features to knowledge about memories of past events in particular locations and the cleverness of animals in taking advantage of various situations. Herders state that the behavior of the flock, near a boundary or other places sheep or goats are not allowed to go, depends on the identity of the herder and the dog(s). If the herder is not the one who did the teaching, the flock may take advantage of the situation and rush into the forbidden place, as often occurs when a trainee cares for the flock. The same can happen when the herder who trained the flock uses different dog(s), which is why experienced herders ask their trainees to herd with the same dog(s). This also occurs when more than one herder tends the same flock in different years. Another common experience of herders has to do with the location where a flock was attacked by wolves. Though this stressful event may have occurred 2 or 3 yr in the past, the sheep still pass quickly through the location, even when a herder makes a strong effort to motivate the herd to graze in that location, which has abundant and palatable forage. The same is true for elk and moose, hunted in particular locations decades or even centuries previously; while the individuals who experienced the hunting events are no longer alive, the behavior remains steadfastly in place by culture passed from one generation to the next

(Andersen, 1991; Mangus, 2011). These "event-memories" or "episodic-memories" can persist for years, a scale recently addressed for mammals and birds through neuroscience and cognition science (Raby and Clayton, 2012). Determining mechanisms that enable animals to remember past events is currently the focus of research and debate (Martin-Ordas et al., 2013).

Step 3: Modulating the "Temporary Palatability Scoring" of Forages

Herders agree that the location and mix of plants in patches, not individual plants, increases or decreases appetite. Thus, herders distinguish different areas that are more or less appreciated depending on the range of forages, on what the animals just ate, and on what they "expect to find afterwards." The notion of "expectation" is related to the herders' interpretation of "contrary behavior" observed during unproductive foraging bouts. This kind of behavior can include a "questioning attitude," when animals prick up their ears, stare wide-eyed in the herder's direction, or bleat. "Sulking" is another form of this behavior, when animals nibble plants they usually ignore while frequently raising their heads to look at the herd's movement.

According to herders, animals develop a "temporary palatability scoring" as they judge, in a comparative way, whether the food offered in an area is satisfactory or not. Herders state that they can successfully modulate this palatability scoring (see "m" in Fig. 4) by organizing sequenced access to distinct grazing patches that allow for minor foraging transitions over several days. It is important to prevent the herd from having a much better foraging experience one day, compared with others, as they will spend most of the other days searching for those forages and fail to use all of the other forages that must be grazed. Thus a herder tries to avoid two situations that lower daily intake: 1) allowing the herd to experience a range of "palatability scoring" much too wide for what will be available during the ensuing season at that particular grazing place, which results in a constantly "frustrated" herd; and 2) restricting the herd to a narrow and overly predictable range of "palatability scoring" that can lead to "grazing weariness."

For example, if a herder lets a flock of sheep graze areas near mountain crests—where plants are young, tender, and very palatable—for the first few days upon arrival at a high-mountain range and then restricts them to the bottoms of mountain slopes—where forages are mature, coarse, and less palatable—the sheep become "frustrated." Likewise, if sheep or goats graze flowering and fruiting leguminous shrubs along forested creeks and then are forbidden from grazing these places, although access to these highly palatable forages was temporary, that experience changes the "palatability scores" of other forages, which leads to "frustration" and less grazing and intake because animals are constantly trying to go elsewhere to forage.

On the other hand, a narrow and overly predictable range of "palatability scores," due to offering the same foods repeatedly, can lead to "grazing weariness." For instance, if a herder makes sheep graze for days on similar swards—grasses and legumes—without also taking them to other patches of different plants, the sheep get "bored," especially sheep that have experienced in previous years the array of forages in the area; they know other forages might be available and they come to dislike the herder. This leads to lower daily intake, as meal durations become ever shorter because sheep are not "boosted" by some diversity when they reach partial satiety for a specific type of forage mix. Day after day, they know the forages and locations will probably be the same, and they rapidly satiate on both the forages and locations.

Between these extremes, herders adjust the herd's "temporary palatability scoring" three ways. 1) They make daily foraging patterns predictable, for example, by ending each evening circuit with the most palatable foods to prevent the herd from searching for them during the day. By so doing, the herder can create different temporary palatability scorings on the basis of the time of day. 2) They make use of different vegetation patches predictable during a day or half-day. Animals learn they will be allowed to use the range of forages in the area during the day, thus limiting their attempts to search for more palatable forages. 3) They ration access to the "best spots" during each grazing circuit to reinforce the herd's reliance on and trust of the herder.

If you ask herders: "Do your sheep like that plant?" most of them answer: "It depends on context." Herders are reluctant to attribute any fixed palatability values to edible plants, except for those that are either extremely palatable or inedible. Between these two extremes, they state that the content and structure of grazing patches, rather than individual plants, are what increases or decreases an animal's tendency to select and eat a certain plant.

Historically in science, the palatability of food items was thought to be static, hence tables that rank preferences for food items. What is palatability? Palatability is a narrowly defined term with vague and simplistic meanings. Webster defines palatable as pleasant or acceptable to the taste and hence fit to be eaten or drunk. Animal scientists usually explain palatability as liking influenced by a food's flavor and texture, or the relish an animal shows when eating a food. Conversely, plant scientists describe palatability as attributes of plants that alter preference such as physical and chemical composition, growth stage, and associated plants. All popular definitions focus on either a food's flavor or its physical and chemical characteristics.

Research of the past 4 decades has redefined palatability as the interrelationship among primary and secondary compounds interacting with cells and organ systems in a dynamic network of communication that unites a body (nervous systems in the brain and gut with the endocrine, immune, and reproductive systems) with the biophysical environment where an organism forages (Provenza, 1995a,b). Feedback from the body to the palate is how cells and organs influence which foods, and how much of those foods, creatures eat. These relationships, mediated by neurotransmitters, hormones, peptides, and gut microbes, are the basis for the nutritional wisdom of the body manifest through the ability to meet needs for energy, protein, amino acids, minerals, and vitamins and to self-medicate (Provenza, 1995a, 1996; Forbes, 1998; Bernays and Singer, 2005; Provenza and Villalba, 2006; Furness et al., 2013; Hagen et al., 2013; Provenza et al., 2015). In essence, the costs and benefits of foraging are translated into the hedonics of flavor on the basis of need. These abilities, which are conserved in species from yeast to human beings (Provenza and Villalba, 2006), are consistent with observations of herders that food preferences depend on the needs of the animal relative to the mix of foods on offer. This functional account of palatability highlights the importance of flexibility to select combinations of forages in environments that change temporally and spatially from scales of minutes to years.

Historically, the herders' notion of "temporary palatability scores" for forages was inconsistent with scientists intent to develop lists of fixed "palatability ranking" for forages (Reid, 1951; Daget and Poissonet, 1972). Recent research confirms what herders insist: this scoring, or ranking, is not fixed within a season or year; it is related to what they "expect" to find at pasture at a certain time of the year—day, week, and season—and to what they have just eaten. Animals get "frustrated" and "weary" when they must eat the same forages repeatedly.

Three hypotheses—one accenting food flavors, another nutrients, and yet another secondary compounds—have been put forth to explain why animals eat a variety of foods and forage in different places. Each of these hypotheses is consistent with the observations of herders that what matters is the mix of foods in time and space, not individual foods, as no one food can meet all of the nutritional needs of animals while at the same time preventing toxicity from eating too much of any one food. Each of these hypotheses focuses on part of a process that is ultimately integrated and dynamic. The satiety hypothesis integrates these three hypotheses and accounts for why, in the herder's parlance, animals "get frustrated or bored with a monotonous diet when they know other forages are available in the area."

Some contend animals eat a variety of foods because they satiate on the flavors of foods *(flavor-specific satiety)*. Livestock prefer foods with different flavors, and their preference for a particular food declines as the food is eaten. Neurons for sight, taste, and odor stop responding to the sight, taste, and odor of a food eaten to satiety, yet they continue to respond to other foods (Critchley and Rolls, 1996). Consistent with these findings, when sheep and cattle eat a flavored food, such as maple- or coconut-flavored grain or straw, they prefer food with the alternate flavor the following day (Atwood et al., 2001a). Animals thus satiate after they eat a particular food, and the degree to which their preference drops depends on how adequate the food is relative to the needs of the individual (Early and Provenza, 1998; Bailey et al., 2015).

Other researchers maintain that animals eat a variety of foods to meet needs for energy, protein, minerals, and vitamins *(nutrient-specific satiety)* (Westoby, 1978). As no one plant contains all these nutrients in the proportions animals require, individuals must eat a variety of different foods to meet their needs for various nutrients. Landscapes with many different plant species, with different rooting depths and mineral acquisitions, enable animals to meet needs.

Yet another explanation for why animals eat a variety of foods emphasizes the need to avoid toxicity from secondary compounds *(secondary compound-specific satiety)* (Freeland and Janzen, 1974). Feedback from secondary compounds limits how much of any one food an animal can eat, as shown for insects, fishes, birds, and mammals (for specific examples with livestock see Dziba et al., 2006; Dziba and Provenza, 2007). Eating small amounts of a wide variety of foods that differ in phenolics, terpenes, and alkaloids—each detoxified in different ways in the body—prevents toxicity while exposing a body to a wide array of primary and secondary compounds useful for nutrition and health (Provenza and Villalba, 2010).

While these hypotheses accent a facet of functionally integrated systems in a body, the satiety hypothesis attributes changes in preference to transient aversions to the flavors of foods that arise as primary (e.g., energy and protein, Villalba and Provenza, 1999) and secondary (e.g., tannins, saponins, and alkaloids, Villalba et al., 2011) compounds interact and feed back to influence liking for the flavors of particular foods (Provenza, 1995a, 1996; Provenza et al., 2015). These interactions cause animals to eat a variety of foods with complementary phytochemical profiles and to forage in a variety of places (Bailey and Provenza, 2008; Bailey et al., 2015). As herders observe, aversions occur when animals eat the same foods too often or in too great an amount. The decrease in preference is stronger and more persistent when the foods are either deficient or excessive in primary or secondary compounds (Early and Provenza, 1998; Villalba et al., 2011). Satiety is thus mildly to strongly aversive depending on the needs of an animal relative to the phytochemistry of the forages on offer in a landscape.

The satiety hypothesis explains why animals eat a variety of foods and why they eat more when offered a variety of foods (for many examples see Provenza et al., 2003; Provenza and Villalba, 2006). Sheep, for instance, have higher total daily intakes of forage when they first eat clover in the morning and then eat grass in the afternoon than if they eat only clover (Newman et al., 1992; Parsons et al., 1994). Hungry sheep prefer clover in the morning likely because it is more nutritious and digestible than grass, but as they eat clover, sheep acquire a mild aversion to clover, which causes them to eat grass in the afternoon; the aversion to clover subsides during the afternoon and evening and by morning the sheep are ready to eat more clover. The transient aversion is likely caused by feedback from primary (organic acids from soluble carbohydrates and ammonia from highly digestible protein) and secondary (cyanogenic glycosides) compounds (Cooper et al., 1995; Lobley and Milano, 1997; Francis, 2003).

Sheep prefer to forage in locations with a variety of foods (Scott and Provenza, 1998), and when they are fed protein and energy imbalanced diets, they forage in locations and on foods that rectify these imbalances (Scott and Provenza, 2000). Eating forages that complement one another is important for increasing forage intake: intake and nutrient utilization diminish with imbalances of energy (soluble carbohydrates) relative to protein (ammonia) (Russell et al., 1992; Sinclair et al., 1993; Hill et al., 2009), while intake increases for forage mixes that produce appropriate ratios of energy and protein (Villalba and Provenza, 1996, 1997a,b,c, 1999; Kyriazakis and Oldham, 1997). Thus animals avoid eating the same old foods in the same old places, which in the herders' words they do to avoid getting "frustrated" or "bored" and the variety of foods on offer in a landscape affects the ability of a body to satiate on needed nutrients. Finally, compared with naïve sheep, experienced sheep eat much more of three foods containing tannins, terpenes, or oxalates—even when they have ad libitum access to highly nutritious familiar foods (Villalba et al., 2004; Shaw et al., 2006a,b). Hence, as the herders well know, past experience, satiety, and variety are linked one with another (Provenza et al., 2003).

Step 4: Designing Grazing Circuits to Create Food Synergies by Meal Sequencing

All herders stress the need to conceive efficient herding circuit for the day or half-day, the latter corresponding to a meal. When we showed them our graphs of meal kinetics (Fig. 2), they were not surprised, with one explaining: "The main thing is to order the animals' encounter with different mixtures of forages to boost their appetite."

For herders, a grazing circuit is a nearly uninterrupted time of foraging over several hours, designed to influence food choices and create food synergies that motivate intake. Herders are convinced it is important to identify the right combinations of "grazing sectors" to be offered in a circuit (see "n" in Fig. 4). They use the term "sector" to describe functional subdivisions of grazing landgeomorphologic features such as a mountain crest, river bank, grassy but rocky slope—with predictable responses to moving and foraging on each sector (Savini et al., 2014; see example at Fig. 5). Changes in behavior occur as the herd moves from one sector to another. Herders focus on the advantages gained by diversifying sectors and fodder resources, while reinforcing both the "temporary palatability scoring" of forages (see "o" in Fig. 4) and respect for grazing boundaries (see "p" in Fig. 4). As the herd must be able to spread out over an individual sector, the minimum area of a sector is related to both herd size and animals' gregariousness. The same grazing area may be carved into several sectors for a herd of 70 goats or used as one sector for a flock of 1 500 sheep. These sectors frequently comprise a number of plant communities, as well as the border areas between them.

Scientists know that livestock make grazing circuits on a daily basis, even when they are allowed to graze freely. First mention of circuits was of arid and semiarid rangelands, where scientists stressed the influence of points of attraction, especially drinking water (Valentine, 1947; Lange, 1969). Dairy cows forage in repeatable circuits on an 8 ha seeded meadow in humid Northern France (Lefeuvre and Leclerc, 1984), and their patterns are influenced by the location of the gate where cows know they will be called for milking in late afternoon. Forages in the half of the pasture near the gate are much more

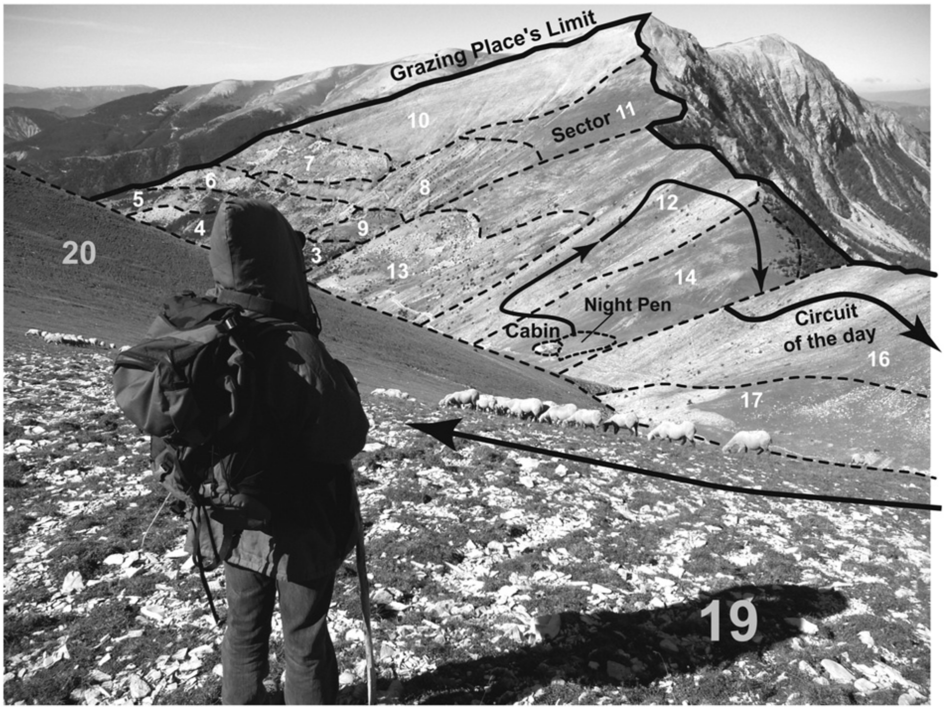

Fig. 5. Description by a shepherd of a portion of his 1200-ha summer grazing place (1100 sheep) in the French Southern Alps. On that day, some of the numbered grazing sectors were used to sequence the grazing circuit and meal (see successive arrows). The circuit started from the night pen located beside the shepherd's cabin (from: Meuret and Provenza, 2015).

heavily used, independent of topography, biomass, and nutritive value. Daily grazing circuits also occurred in winter when sheep in Utah were offered eight species of shrubs planted in patches over 2 ha of crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.): sheep foraged on sagebrush (*Artemisia tridentata* ssp. *vaseyana*) in the morning, crested wheatgrass and other shrubs throughout the day, and fourwing saltbrush (*Atriplex canescens* (Pursh) Nutt.) in the evening (Gade and Provenza, 1986).

In wild herbivores and domestic livestock, social organization may lead to rotational grazing without fences, a notion based on four assumptions (Provenza, 2003a; Shaw et al., 2015): 1) many social herbivores live in extended families, 2) maintaining the cohesiveness of families and their home ranges influences behavior, 3) individuals within families differ in their preferences for foods and habitats, and 4) families maintain their unique identities by avoiding prolonged contact with other families. Movement of families across landscapes enables animals to eat a broader array of plants and to forage in a variety of locations as individuals maintain the cohesiveness of the group and accommodate different preferences for forages among individuals within a family (Bailey and Provenza, 2008). Interactions among families may increase movements across landscapes as different families avoid prolonged contact with one another. Hence, diet and habitat breadth both may increase through social organization and culture, which may maintain the health of individual animals and biodiversity of landscapes.

Grazing circuits also enable each individual in a family to select plants that best meets its needs (Provenza et al., 2003). Differences among individuals in food preferences depend on variation in form and function, and marked differences are common even among "uniform" groups of animals in needs for nutrients (Scott and Provenza, 1999) and abilities to cope with secondary compounds (Provenza et al., 1992, 1999). Thus variation among individuals can affect productivity of the group if the diet diverges much from what individuals at the extremes—which can be as much as half of the group—prefer and can tolerate (Provenza, 1996; Scott and Provenza, 1999; Atwood et al., 2001b). Herders continually provide the flock with a variety of foods that generates possibilities for each individual to eat combinations of foods that create synergies and thus enhance intake. As the herders say, "[We want] to let each of our sheep select what it prefers to eat at this moment in the grazing circuit."

Ten experienced herders co-conceived with us a model to help fashion daily circuits (MENU; Fig. 6) (Meuret, 1997). When intake must be motivated for a "target-area" (square in center of Fig. 6) consisting of less palatable vegetation, for instance coarse grass or scrub to be cleared, the herder identifies and uses complementary, sometimes contiguous, grazing sectors. The herder assesses sectors according to two criteria—relative abundance (y axis) and relative palatability (x axis) of vegetation—that can play one of six roles.

At the beginning of a circuit, the choice of a sector depends on the herd's appetite. If the herd lacks appetite, the herder takes the animals to graze a sector of highly palatable, though not necessarily abundant, forages (see "Appetite Stimulator" sector, Fig. 6). Conversely, the herder may take the herd to a sector with abundant but much less palatable forages ("Appetite Moderator" sector). When the herder considers that the rate of foraging has stabilized, he takes the herd to its first course on the "Target-area" (center of model). Palatability and abundance in this sector are a benchmark such that all other sectors are evaluated relative to this one. After 1 to 2 h, the herd's foraging activity in this sector often slows. The animals have "been there, done that," say herders, and they get "bored" with the average quality of resources available.

Herders use a "Booster sector" to renew appetite. Two types of "booster" phases allow the herd to forage briefly, one in a highly palatable sector (B_1 in the model) and the other in a poorly palatable sector (B_2 in the model). The goal of the latter is to make the herd understand that the target area is not that bad, relatively speaking. To avoid adverse effects of anticipation on foraging behavior and intake, this phase of a meal must not be predictable and is limited time-wise, for instance, from 15 to 45 min with 50 goats on woody rangeland during a meal of 3 h, or 30 to 50 min with 2,000 sheep in high-mountain pasture during a meal of 5 to 6 h.

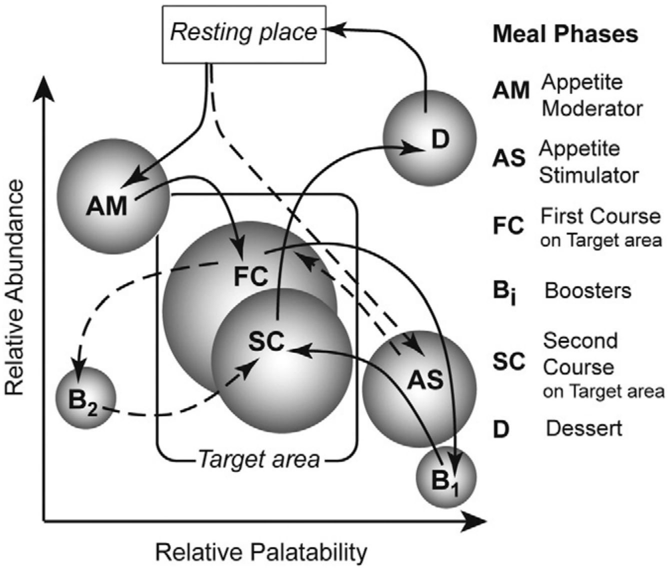

Fig. 6. The MENU model offers herders a way to plan a half-day grazing circuit that stimulates the herd's appetite for forages in a "target area" (center), which would not otherwise be palatable for the herd without his interventions. The herder uses pasture diversity— relative palatability and abundance of food—to conceive an effective sequencing of distinct grazing sectors, which correspond to meal phases.

After this, a herder can return the herd to the target area to continue the meal with a "second course." This sector can be located next to that of the "first course" and be similar in nature. Nonetheless, as the herd nears the end of the meal, it is important to provide something "slightly better." At this point, the herder estimates the time the herd has spent eating and assesses satiety. If the herd is not satiated, and the time remaining will not allow him to carry out a new "course-booster-course" sequence, he can use a "Dessert sector." The goal of the dessert sector is to ensure rapid intake over a short time by offering forages that are highly palatable and abundant. It is of greatest importance that the herd not be able to anticipate the dessert phase, which can markedly decrease intake during prior meals. The herder ensures the unpredictability of the dessert phase by making use of dessert sectors at irregular intervals. Some herders say: "It takes 2 wk for them to understand that waiting for dessert is a waste of time."

The example circuit in Fig. 7 illustrates the impact on the instantaneous intake rate (minute scale) on a focal dairy goat in a herd of 39 goats foraging in summer on downy oak (*Quercus pubescens* Willd.) coppice. There were four meal phases, with roles assigned from MENU. Oak foliage, offered in two phases, was the bulk of the meal. Midway through the meal, a highly palatable leguminous shrub (*Hippocrepis emerus* L.) was used to boost appetite. Nineteen plant species contributed to the meal, among the 62 edible forages. The instantaneous intake rate (IIR) was high, increasing by more than 10 g DM min^{-1}. The accelerations of IIR were often the result

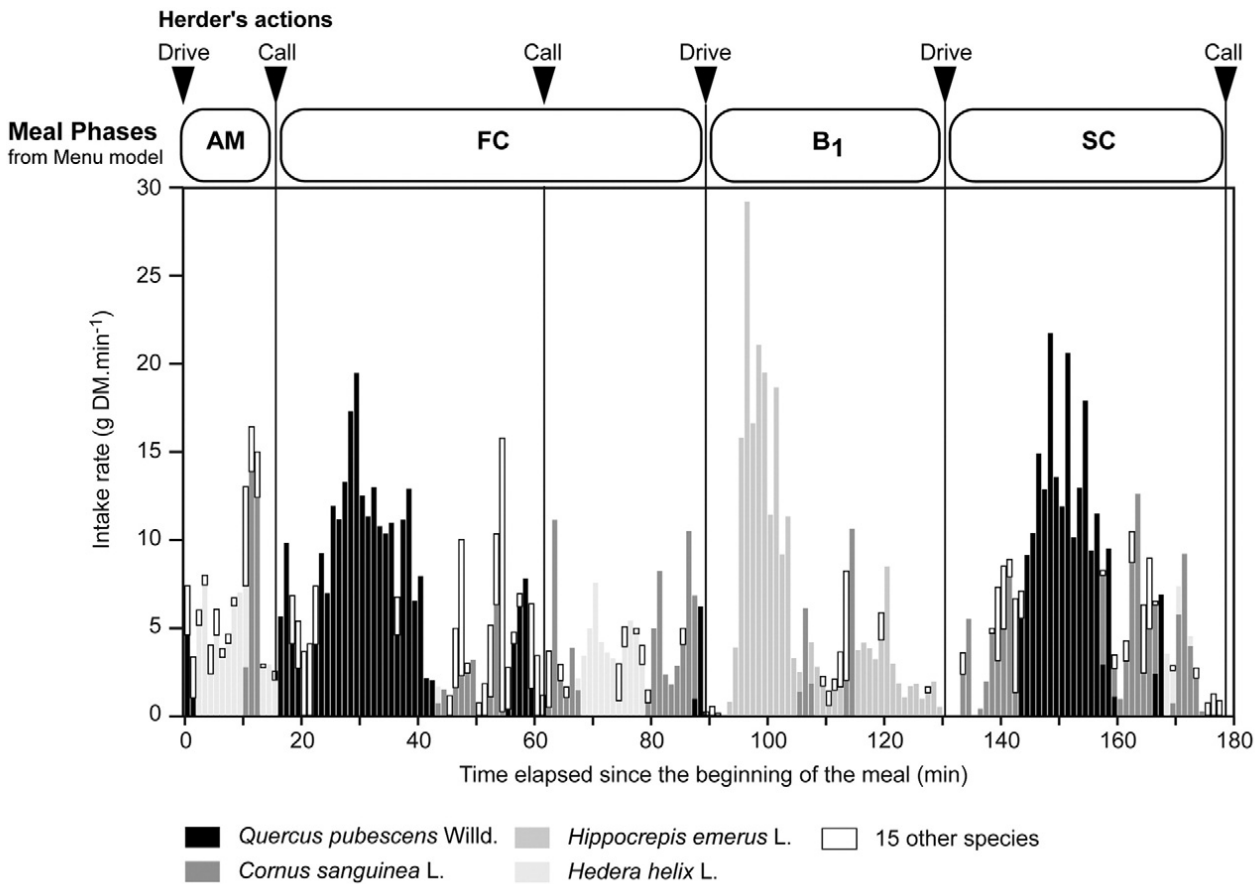

Fig. 7. Variation in instantaneous intake rate for a focal animal during a 3-h meal of Alpine dairy goats herded in Mediterranean oak coppice. To stimulate appetite, the herder used an effective sequence of grazing sectors to structure the meal into four distinct phases using roles assigned from the MENU model (top of the graph). Significant accelerations in instantaneous intake rate were often a result of the direct actions of the herder, especially when moving the herd from one grazing sector to another (see black arrows on top of the graph).

of the herder's actions (see arrows, top of graph), which prompted the herd to travel short distances to graze another sector (Meuret et al., 1994).

Inspired by the results of the research with herders in France, scientists have discovered that the synergies herders describe within circuits and meals depend importantly on interactions among primary and secondary compounds in time (when a meal is eaten) and space (where a meal is eaten). For instance, cattle steadily decrease time eating endophyte-infected tall fescue if they first graze tall fescue alone for 30 min followed by birdsfoot trefoil (*Lotus corniculatus* L.), alfalfa, or alfalfa-trefoil combination for 60 min (Lyman et al., 2011, 2012). Conversely, when the sequence is reversed, cattle forage actively for 30 min on trefoil, alfalfa, or trefoil-alfalfa combination and then forage actively on fescue throughout the 60-min meal. These patterns of foraging are similar with high-alkaloid reed canarygrass (*Phalaris arundinacea* L.). Likewise, lambs first fed high-saponin alfalfa or high-tannin birdsfoot trefoil for 30 min, followed by a 3.5-h meal of either endophyte-infected tall fescue (alkaloids) or reed canarygrass (alkaloids), eat more and they digest more dry matter, nitrogen, and energy than lambs not first provided with alfalfa or trefoil (Owens et al., 2012a). Offering lambs a first course of alfalfa or trefoil increases intake and as a result increases the amount of nutrients digested. These benefits are achieved when lambs eat less than 30% of their daily intake as alfalfa and less than 13% of their intake as trefoil; hence, the value of "appetizer" and "booster" phases herders use to stimulate intake.

Meal sequences enhance intake by creating synergies among primary and secondary compounds, which enhance detoxification (reviewed in Provenza et al., 2003; Provenza and Villalba, 2006). Sheep eat more food with terpenes when they first eat food with tannins (Mote et al., 2007, 2008). These findings are consistent with studies that show sheep with a preference for sagebrush, a shrub high in terpenes, eat more bitterbrush (*Purshia tridentata* [Pursh] DC.), a shrub high in tannins (Seefeldt, 2005): bitterbrush as an "appetizer" positively impacts their appetite for sagebrush. Likewise, when sheep and goats first eat forages high in energy or protein they subsequently can eat more of foods with terpenes (Banner et al., 2000; Villalba et al., 2002a), tannins (Villalba et al., 2002b), and saponins (Williams et al., 1992; Martinez et al., 1993). By enhancing detoxification processes, energy and protein better enable goats, sheep, and cattle to eat more sagebrush (Villalba et al., 2002a; Villalba and Provenza, 2005; Dziba et al., 2007; Petersen et al., 2014). In the same way, herders enhance intake by offering dairy goats a 20 to 25 min course of lucerne or leguminous shrubs such as scorpion senna (*Hippocrepis emerus* L.) followed by a course of oakbrush (*Quercus pubescens* Willd.). Cattle foraging on sagebrush or endophyte-infected tall fescue first eat the bark or trees high in tannins (Petersen et al., 2014); tannins in bark or shrubs like bitterbrush and oakbrush or forbs like birdsfoot trefoil and sainfoin (*Onobrychis* spp.) enable herbivores to cope with terpene- and alkaloid-rich foliage of plants by binding with terpenes and alkaloids; tannins in forages like trefoil and sainfoin also reduce ammonia (Tanner et al., 1995), which enables sheep to eat more trefoil and sainfoin (Owens et al., 2012a,b). In these cases, the various forages eaten in circuits as "appetizers" or "boosters" enable animals to use dominant but coarse forages like sagebrush or oakbrush. Finally, sheep infused with saponins, and then allowed to choose among alfalfa, trefoil, and tall fescue, decrease preference for alfalfa (saponins) and increase preference for trefoil (tannins) and tall fescue (alkaloids); conversely, lambs infused with alkaloids decrease preference for tall fescue, while lambs infused with tannins increase preference for tall fescue (Villalba et al., 2011).

Furthering the Exchange Between Herders and Scientists

We have highlighted insights gained by researchers made through relationships developed with herders in France. We described how herders teach their animals to use the full range of forages and then establish daily grazing circuits to stimulate appetite and intake. Through hands-on experience, herders have come to understand the many processes involved in food and habitat selection by livestock. We reviewed scientific studies that are consistent with the experiential knowledge and practices of herders. We now highlight some opportunities to further create and share knowledge among scientists and herders, with the aim of better understanding still poorly informed processes in science and contributing to better appreciate herders' knowledge in managing rangeland resources at the landscape level.

Time: A Key Variable for Future Studies of Foraging Behavior on Grazing Lands

In foraging science, time is the least studied variable in grazing behavior. Rates of metabolism have been of interest in studies of kinetics in nutrition and toxicology. Studies of ingestive behavior use time (bite rate and grazing time) and nutrient kinetics (primary and secondary compounds) with forages on pastures. However, scientists have not studied how the amount of time allotted to a course in a meal influences intake in subsequent courses (but see Meuret et al., 1994; Agreil et al., 2006; Bonnet et al., 2015). Herders' practices are encouraging researchers to consider time as a crucial variable for appraising the value of grazing lands: from multiyear transgenerational learning to selecting plant parts within a meal.

As shown with MENU, the key to this value is the schedule involved in the feeding process and the proper mixing of forages. This "value" is created by the herder through effective use of grazing sectors in time and space. Given the same territory and time of the year, the same breed of livestock, the same size herd, and the same stocking density, no two herders will obtain the same feeding values from the area because their animals will not forage with the same appetites. Success depends on the herders' ability to design and then adjust circuits over time and space. As a consequence, a scientist seeking to identify the various grazing sectors and their foraging functionalities must undertake an analysis of the territory allotted to the herder, using a scientific approach that is closer to landscape ecology than to forage crop agronomy.

Mixing Primary and Secondary Compounds in Diets

Most herders are aware that daily grazing circuits that combine young plants with mature and fibrous plants create synergies, and they know these relationships are more complex than merely primary compounds. They appreciate the many nutritional and medicinal values of plants and plant diversity. They know the most elementary principle of toxicology: Every plant can be toxic depending on the time and amount eaten. They are interested in plant combinations that boost appetite, with attention to the process of intrameal detoxification patterns.

As a condition for the success of this further exchange, knowledge about secondary compounds must be presented in ways that fit with herders' practices. Yet another avalanche of lists of individual plants with secondary compounds—as a function of plant phenology, time of day, and season—must be developed into functional categories of plant mixes that a herder can sequence within circuits to enhance appetite and limit overfeeding on toxic metabolites. That can encourage herders to diversify and sequence distinct mixes of plants within circuits, give meaning and better understanding to observations of food choices that they cannot interpret for now, and renew their curiosity about plant mixtures in grazing sectors, while trying to favor the right mixing of primary and secondary compounds within daily diets.

Studies of self-medication with secondary compounds are in vogue, and herders would be highly interested to participate with their own experiential knowledge. During our interviews, none of the herders referred to "secondary compounds" in plants and diets, but some say "self-medication should occur" on rangeland on the basis of their frequent observations of temporary preferences for atypical foods such as dried nettles (*Urtica dioica* L). Most herders practice homeopathy and natural plant remedies for themselves and their animals for three reasons. The cost for a veterinarian, if there is one knowledgeable in ruminants, to come from the nearest town is more than the price of a sheep or goat. Herders have accumulated years of experiences caring for the health of the herd, including giving urgent care to individuals in the mountains or when the herder is alone with the herd. They use homeopathy and herbal medicines such as essential oil flasks (e.g., oil of *Lavandula angustifolia* to cure abscesses and ward off flies; *Arnica montana* for use after trauma), which are easy to carry in a shepherd's bag.

Lowering Stress: A Shared Stake Between People and Animals

Most herders are convinced it is of upmost importance for them to stay in front of the herd, and sometimes lateral to the herd, and to be more or less closely followed by the animals with mutual confidence. What is called a "round-up" in the United States is quite different in France: A call of the herder, with his dog mute at his feet, is followed by silence; then the sheep or goats raise their heads from foraging and begin to move in the herder's direction. If needed, they occasionally use dogs as "bad cops" to push some animals from behind.

French herders do not discuss "low-stress handling," but they link the stress of animals with that of the herder or farmer. "On my arrival day, I can tell you about the stress level of this farmer just by looking at his sheep!" said one shepherd. Many shepherds point out that, at the end of a grazing season, a farmer may say: "What happened? I don't recognize my sheep. They are all very calm." Usually, the shepherd can't easily explain why. He just came from 3 to 5 mo of herding involving constant attention building a mutual relationship with the herd.

On rangelands, low-stress techniques for moving and settling animals are now in fashion (Smith, 1998; Cote, 2004; Hibbard, 2012). While some livestock farmers, as well as some herders, do not appreciate the value of these relationships for minimizing stress and upgrading grazing management and animal performance, ranchers who have adopted these practices highlight the benefits for working conditions and animal performance. In science, welfare mostly refers to stress on animals created on farms and in confinement, though Porcher (2006, 2011) explicitly shows that well-being or suffering in livestock should be considered as a shared stake between working people and animals. These interactions are not merely about stress. Rather, they are about creating relationships among human beings, animals, and the landscapes they inhabit.

Creating Good Relationships with Animals That Are Socially Structured

Herders refer to "the herd" as its own being with a collective behavior unto itself. The behavior of the group emerges from the collective behaviors of individuals. Nonetheless, in both livestock (and human) systems and science, social effects were not seen as integral but often considered "external constraints" for nutrition, health, and production. For decades, behavioral science focused on social hierarchy and dominance studies, as initiated by Schjelderup-Ebbe (1922) with chickens, despite results from studies of wild animals in natural habitats that showed social interactions are far more complex and dynamic than those of animals in confinement (Rowell, 1974; Despret, 2008). In free-living conditions, the notion of a "stable social hierarchy" is now considered erroneous for most mammalian species, including wolf packs (Mech, 1999).

Herders frequently refer to animal individualities and temperaments, concepts of growing interest in behavioral ecology (Stamps and Groothuis, 2010). "Charismatic leaders," a term suggested by Power (1991) and Despret (2006), must understand quickly what a herder expects of the flock, and they must have leadership so that their peers will follow them. A large flock of sheep often requires 12 to 24 "leaders." In transhumant flocks, herders traditionally use castrated male goats and rams, equipped with a king-size sheep bell, as efficient "menons" (guides).

For his part, a herder must behave appropriately to be accepted as the uncontested leader by the flock. His/her authority level depends on a herder's temperament and herding style and on context including an animal's previous experiences, landscape characteristics, and weather conditions. Herders state that managing a grazing circuit consists of alternating phases of control and "laissez faire" (Savini et al., 2014), in which the herder acts as a "substitute matriarch," staying sometimes in front of the flock, other times lateral to the flock, more or less closely followed by the sheep with mutual confidence and at the proper pace.

There are opportunities for scientists and herders to collaborate to better understand and model how herders cope with the diversity of animals in a large herd, while using subgroups and individuals as functional entities for actions regarding food and habitat selection (Searle et al., 2010). Functionality could be assessed through the analysis of herders' criteria and their ability to anticipate the behavioral and production responses of subgroups, the latter influenced by distinct breed and levels of food demand, but also and mostly by previous grazing experiences.

Early Learning Process in Animals

Most herders work with animals in late pregnancy, especially with sheep at the end of summer and early fall in the high mountains. Some of them are also hired by farmers during lambing in late fall, winter, and early spring. They are aware that experience early in life influences the foraging behavior of adults, but they seem unaware that these experiences begin in utero and that the experiences of pregnant sheep in late summer can influence preferences and performance of the next generation. To our knowledge, the same is true for farmers: they do not ask the herders to diversify the foods offered during late pregnancy because that will improve the ability of their flocks to use the full range of fodders on the landscape.

When we discuss scientific results about learning in utero with herders, they are interested but not surprised, as they have experienced transgenerational effects within a herd and they are convinced animal "culture" is developed through grazing management. In practical terms, herders tell us they can easily find grazing sectors for pregnant animals to eat more diversified diets than those found on sectors made of natural meadows. With regard to research, scientists have just begun to explore how experience in utero with various mixtures of forages affects preferences for and abilities to efficiently use landscapes. Thus there are opportunities for scientists and herders to collaborate to better understand how experiences with diverse forages in utero affect foraging behavior, performance, and health throughout life and to link those behaviors with the quality of milk, cheese, and meat for human consumption.

Learning to Manage Grazing for Multiple Benefits

Short-duration and management-intensive grazing emphasize the need to intensify management to modify food- and habitat-selection behaviors (Savory, 1983; Gerrish, 2004). To control grazing, livestock farmers and pasture managers using either approach rely primarily on electric fencing, with more recent interest in "virtual" fencing, to increase diet and habitat breadth by controlling how long pastures are grazed (time), when pastures are grazed (timing), and the location (where) of grazing. As valuable as fences can be, they can't replace a herder's knowledge and constant daily attention to orientate grazing on rangelands.

By designing grazing circuits, a skilled herder can encourage the flock to use different forages that vary in palatability. Some of the greatest innovations in grazing come when a flock learns to eat an array of plants, from desirable to undesirable, during the day across the landscape. Herding is thus relevant for targeted grazing, as shown with "Target area" from the MENU model. Herding also can be used to improve habitat for wildlife. For instance, herders can design grazing circuits that improve habitat by increasing annual and perennial plants and insects to provide brood-rearing habitat and residual nesting cover for sage grouse and that don't rely on fences, which pose hazards to sage grouse and are expensive to build and maintain (Guttery, 2010; Petersen et al., 2014). Proper herding with use of dogs can also deter predators of livestock, including reintroduced gray wolves in Wyoming, Montana, and Idaho. Finally, herding can create a close relationship among livestock, human beings, and landscapes, which largely has been lost as we've come to rely on fences as "livestock-sitters" to manage grazing. In a sense, herders can be "ecological doctors" who care for the health of the land.

Management Implications

In this synthesis, we explore the relationship between science and art to emphasize how different ways of knowing can support and enrich one another, in the case of grazing, the complementarity between the experimental knowledge of scientists and the experiential knowledge of skilled herders. Both the science and the practices emphasize flexibility in the face of ever-changing environments. The knowledge gained by both groups has implications for managing grazing on rangelands and pastures, and the principles and practices provide insights into ways to successfully target grazing on specific plants and habitats. The science highlights the importance of learning from mother and peers, as well as nutritional complementarities among forages, on diet and habitat selection. The hands-on experiences of herders validate these findings and emphasize practical dimensions important for managing grazing animals. The use of grazing circuits and proper timing of daily access to "focal points of attraction," such as water, foraging, and resting places, are key for increasing feeding motivation of animals on rangeland; for creating synergies between distinct sectors of pasture and plants that can overcome lack of palatability of forages; and for enhancing plant biodiversity across landscapes that enables individual animals to select diets that enhance appetite, performance, and health.

Finally, most herders in France, especially young ones, are French people from urban backgrounds, with rural roots increasingly far behind them. Five schools in France collectively train half of the people who want to become herders (Jallet et al., 2014). Between sessions at school, training emphasizes hands-on experience in real-life situations, where trainees learn from experienced herders, who teach trainees how to enhance animals' appetite through grazing circuits. For herders, learning consists of trying, adjusting, and making mistakes without becoming demoralized and considering as both challenge and opportunity the absence of scientific and technical norms about herding. Generally, herders are reluctant to apply technical recipes and they are doubtful of knowledge and prescriptions that come from science. They know about how much traditional agronomy and animal sciences have succeeded in disqualifying their own knowledge as being far too "subjective" (Hubert et al., 2014).

To further the exchange with herders, who are generally reluctant to embrace prescriptions that come from scientists, we share our experiences with them. Most herders forget their reluctance if a scientist empathizes and validates their endless curiosity about animals and plants and their enthusiasm to be creative. When a scientist avoids dispensing recipes and prescriptions, and instead explains his or her scientific approach—paradigms, methods, conditions, trials, errors, unexpected results—herders of all ages empathize and forget their reluctance of science. In partnership, scientists and herders can better understand principles and processes and link them with decision-making practices: preemptive and creative management within the framework of distinctively personal goals.

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