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LIVESTOCK FEEDING ECOLOGY AND RESOURCE UTILIZATION IN A NOMADIC PASTORAL ECOSYSTEM

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SUMMARY

(1) Seasonal patterns of forage selection, diet diversity, and habitat use were quantified for livestock managed by the Ngisonyoka Turkana in arid north-western Kenya by direct observation of free-ranging herds. The objective was to characterize the trophic niche segregation of livestock and their potential harvesting capacity for the heterogeneous vegetation resources of this ecosystem.

(2) Cattle and camels were grazing and browsing specialists, respectively, while goats, sheep, and donkeys were generalists for both herbaceous and non-herbaceous vegetation.

(3) Diet and habitat use were greatly influenced by season. Relative to brief rainy periods of resource abundance, long dry intervals of resource scarcity were times of reduced diet diversities (forage-class basis) for most species and greatly increased variation in habitat use. Livestock generally exhibited the greatest diet similarity in dry periods but were most segregated in terms of feeding habitats during these times.

(4) The livestock in aggregate provided a very broad, opportunistic, and temporally stable trophic niche that resulted from equitable use of all forage classes, and their mobility provided a means to exploit the entire region. These attributes are essential for the persistence of nomads in this harsh, unpredictable environment, and are inimical to development tactics that serve to reduce livestock species diversity or restrict mobility.

INTRODUCTION

The vast majority of the world's grazing lands occur in seasonal environments that are characterized by marked fluctuations in resource abundance. Among the most dynamic are the arid and semi-arid regions of tropical Africa, where extended periods of dryness are punctuated by erratic rainfall and brief eruptions of forage production. Consumers that are highly opportunistic appear best able to persist in such environments (Jarman & Sinclair 1979).

It is generally accepted that traditional pastoralists exemplify opportunism through their reliance upon diverse herds of mobile livestock, yet there have been few attempts to document the utility of mixed-species associations for environmental exploitation. As part of an interdisciplinary investigation of the Ngisonyoka Turkana in north-western Kenya (Little *et al.* 1984), this research focused on fundamental aspects of feeding ecology to determine the degree to which camels (*Camelus dromedarius*), cattle (*Bos indicus*), goats, sheep, and donkeys provide complementary options for resource use. Seasonal patterns of forage selection, diet diversity and habitat use were quantified for each livestock species as well as for the average aggregate holdings of four Ngisonyoka families. Diets were expected to be different, given the great diversity of vegetation in this system and the varied body sizes, mouth morphologies, and gut anatomies of these species which elicit distinct food-selection tendencies (Janis 1976; Kay, Engelhardt & White 1980; Schwartz & Ellis

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1981). Diet diversity based on forage classes was used to compare trophic niche breadth among species; this was postulated to be inversely related to body size (Schwartz & Ellis 1981) and narrowest for all species during dry periods when forage abundance and diversity is greatly reduced (Jarman 1971; Leuthold 1978). In addition, the cumulative niche breadth of the aggregate herd was expected to be wider and less seasonally dynamic compared with that of constituent species. Seasonal patterns of niche segregation in terms of diet and/or habitat use were hypothesized to resemble those of native ungulate communities in which overlap is lowest during intervals of resource scarcity (Jarman 1971; Leuthold 1978; Jarman & Sinclair 1979).

STUDY AREA

Ngisonyoka Turkana (7500 km^2) lies in the Rift Valley between 1 ° and 3 °N latitude and is roughly bounded by the Turkwell River to the west and north, the Kerio river to the east, and the Turkana District boundary to the south. It is the communal home for approximately 9600 pastoralists dependent upon 59 000 goats, 26 000 sheep, 9800 camels, 9800 cattle, and 5300 donkeys (Ecosystems Ltd 1983) for provision of milk, meat and blood (Galvin 1985). Precipitation is highly variable, but most (>60%) occurs from April to June and annual averages range from 150 to 600 mm in the north and south, respectively. Mean daily temperatures average 30 °C with a variation of 12 °C. The landscape is very heterogeneous, with elevations from 370 m on the northern plains to over 2100 m on the highest peaks of the Kamarok Mountains. These Precambrian mountains bisect the area from north to south and are flanked by unconsolidated Quaternary sediments on both sides. The sediments end abruptly at extensive Tertiary basaltic lava flows, which comprise most of the eastern half of Ngisonyoka.

There are a variety of vegetation types. Low-biomass communities occur on sandy, gravel and lava plains and are typified by savannas dominated by annual grasses (*Aristida* L., *Eragrostis* Host. spp.), annual herbs (*Gisekia* Linn., *Tribulus* L. spp.), dwarf-shrubs (*Indigofera* L., *Sericocomopsis* Schinz spp.), and trees (*Acacia* L., *Commiphora* Jacq., *Boscia* Lam. spp.). Higher biomass is found in mountain savannas and ground water woodland communities which occur along the numerous drainages that originate in the central mountains and dissect the sandy plains. Total net primary production (NPP) averaged throughout the region for 300 mm of rainfall has been calculated to be 167 g m^{-2}; 67% was contributed by grasses and herbs, 28% by shrubs and trees, and 5% by dwarf shrubs (Coughenour *et al.* 1985). Most NPP occurs during the brief wet season, and the remainder of the year is characterized by progressive declines in water availability and large reductions in forage biomass and greenness, changes that are very rapid for grasses and herbs and least evident for large trees (Coppock 1985). More description is provided elsewhere (McCabe 1983; Little *et al.*, 1984; Coppock 1985).

METHODS

Data were collected from April 1981 through July 1982 during two wet and three dry periods in sequence. This was considered a time of above-average rainfall and forage production by Ngisonyoka informants. The sample population consisted of the herds of four households which were visited for several weeks during each period. The livestock were corralled nightly at homesteads and taken to feed or water at herder-determined locations by day. Except for sheep and goats, which were herded together, livestock were managed in species-specific associations. Herders always accompanied sheep, goats and camels and usually accompanied cattle. Only donkeys were always unattended and they usually roamed within the immediate vicinity of the homestead. The aggregate herd for the average family of twenty-one was fifty camels, fifty cattle, seventy sheep, 200 goats, and sixteen donkeys.

Data were collected by accompanying herds on foot during 75 day-long (12- to 15-h) excursions evenly distributed across species and seasons. The bite-count method (Wallmo & Neff 1970; Baker & Hobbs 1982) was used to quantify the food selection of 155 adult animals (roughly six per species per season) in 2-h feeding trials and nearly 350 000 bites were observed. The plant species and parts selected were noted on a hand-held tape recorder, as was the site type in which the bites occurred. Plants were categorized to forage classes which included (i) herbaceous monocots (grasses); (ii) herbaceous dicots (forbs or herbs); (iii) dwarf shrubs; (iv) leaves and stems of larger shrubs and trees; and (v) seeds and seedpods of woody plants (largely *Acacia tortilis* (Forsk.) Hayne subsp. *spirocarpa* (Hochst. ex A. Rich.) Brenan). Sites were categorized by substrate (sand, gravel, lava), terrain (plains, hills, mountains), and position on the plains with respect to water flow (drainage, interdrainage). The sandy plains interdrainages covered 32% of the study area, followed by the lava plains interdrainages (19%), lava hills (18%), gravel plains interdrainages (17%), and the basement-complex mountains (9%). Drainages in total comprised only 5%.

Sites typically varied more in NPP and plant species composition than in forage-class representation. Among low-elevation sites the sandy drainages showed the greatest herbaceous NPP and the highest densities of large woody plants, while sites at higher elevations tended to have more herbaceous NPP than the plains (Coppock 1985; M. B. Coughenour, unpublished data).

Botanical composition of diets was calculated on a dry-weight basis that included estimation of bite weights and bite frequencies following the procedures of Baker & Hobbs (1982). The seasonal diet composition of the aggregate herd was calculated as the sum of diets for all species except donkeys, which were excluded because of their very minor role in food production (Galvin 1985); they are principally used as beasts of burden. These calculations reflected variation in bite sizes and bite rates among species as well as differences in herd sizes.

Diet diversity (H') was calculated seasonally on a forage-class basis for each livestock species and the aggregate herd using the Shannon–Wiener index (Shannon 1948; Hurtubia 1973), which has a lower limit of 0·0 and an upper limit of 0·70 in this instance. Seasonal niche overlap among pairs of livestock species in diet composition and habitat use was calculated separately using the modified Morisita index (Horn 1966). This overlap coefficient ($\hat{C}_\lambda$) ranges from 0·0 for distinct comparisons to 1·0 for complete similarity. Total trophic overlap was calculated by multiplying the respective diet and habitat Morisita coefficients. The effects of livestock species and season on forage-class composition of diets and diet diversity were analysed using the two-way analysis of variance. Tukey's H.S.D. procedure (Steel & Torrie 1980) was used to determine significant differences among means.

Diet information presented here is intended to provide an overview. Important forage species are described in Coppock (1985).

RESULTS

Diet composition and diversity

Diet composition varied considerably among livestock species and changed with season (Fig. 1). Calculated across all seasons, the diet composition for total herbaceous, dwarf shrub, and all other browse forages (including seeds and seedpods), respectively, was (i) cattle (96%, 4%, 0%); (ii) donkeys (71%, 28%, <1%); (iii) sheep (67%, 28%, 5%); (iv) goats (36%, 27%, 37%); and (v) camels (5%, 72%, 23%). Cattle and camels were grazers and browsers, respectively, while goats, sheep, and donkeys were mixed feeders on herbaceous and non-herbaceous vegetation. Diet composition changed significantly ($P \leqslant 0{\cdot}01$) with season for all livestock except cattle. The most notable shifts between the wet and dry periods included increased use of grasses and seedpods relative to dwarf shrubs and browse by goats and increased use of browse relative to dwarf shrubs by camels (Fig. 1a, e). Patterns for sheep were similar to those for goats, though less pronounced, while donkeys typically switched between grasses and dwarf shrubs depending on the

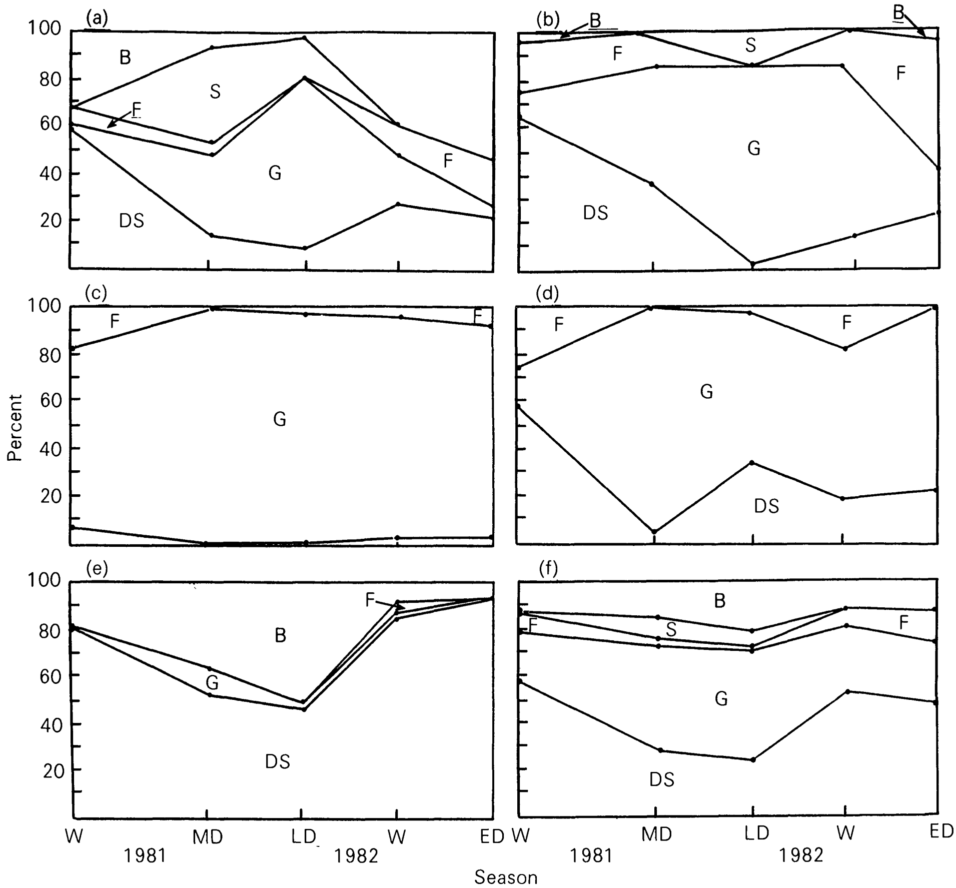

FIG. 1. Seasonal forage-class compositions (dry weight basis) for diets of (a) goats, (b) sheep, (c) cattle, (d) donkeys, (e) camels, and (f) the aggregate herd (excluding donkeys) in Ngisonyoka Turkana during 1981–82. Forage is coded as G (grasses), F (forbs), DS (dwarf shrubs), B (large browse plants), and S (seeds and seedpods). Seasons are coded as W (wet, April–May), ED (early dry, June–July), MD (mid-dry, August–October), and LD (late-dry, November–March).

relative abundance of each (Fig. 1b, d). The annual diet composition of the aggregate herd showed an equitable use of total herbaceous (39%), dwarf shrub (42%), and other browse (19%) vegetation that was generally less seasonally variable than the diets of constituent species (Fig. 1f).

Patterns of diet diversity significantly varied ($P \leqslant 0{\cdot}01$) among livestock species and seasons (Fig. 2b). Cattle, donkeys, goats and sheep tended to have more varied diets during wet and early dry periods than during mid- or late-dry intervals. Camels, however, showed the opposite trend as their diets were most diverse during the late-dry season. In contrast to individual species, the diet diversity of the aggregate herd remained relatively constant (and higher) throughout the year (Fig. 2a). Overall, the diet diversity of the aggregate herd ($\bar{x} = 0{\cdot}53$) was 76% of the maximum possible value (0·70) and ranged from nearly 2 to over 6 times the annual means for goats (0·29) and cattle (0·08), respectively, which bounded the interspecific variation (sheep ($\bar{x} = 0{\cdot}28$), donkeys ($\bar{x} = 0{\cdot}24$), camels ($\bar{x} = 0{\cdot}19$)).

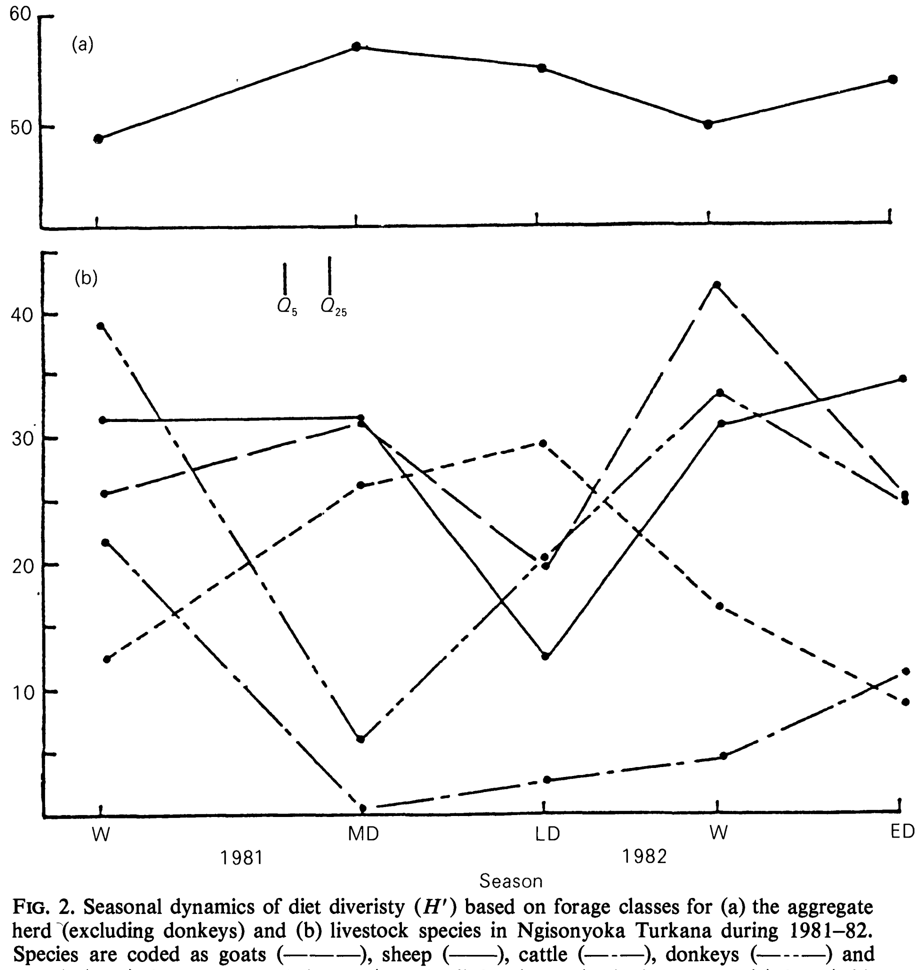

FIG. 2. Seasonal dynamics of diet diveristy (H') based on forage classes for (a) the aggregate herd (excluding donkeys) and (b) livestock species in Ngisonyoka Turkana during 1981–82. Species are coded as goats (— — —), sheep (——), cattle (—·—), donkeys (—·-—) and camels (- - -). Seasons are coded as W (wet, April–May), ED (early dry, June–July), MD (mid-dry, August–October) and LD (late dry, November–March). For (b), any two points on the same line or within the same season separated by a vertical distance greater than or equal to Q_5 are significantly different ($P \leqslant 0{\cdot}01$). Similarly, Q_{25} can be used to compare any two points in (b).

Habitat use

The Ngisonyoka exhibited a seasonal pattern of regional land use. Households were aggregated into large neighbourhood associations throughout the wet and early dry periods (April–July), and these were located on the sandy plains adjacent to the central mountains. Families dispersed during the remainder of the year and returned to the sandy plains with the advent of rainfall the following April. Families moved an average of 8 km every 24 days, and treks of over 70 km during seasonal transition periods were common (McCabe 1983, 1984).

This pattern is reflected in livestock habitat use (Fig. 3). All species typically fed on drainages and interdrainages on the sandy plains from April to October until forage was depleted and local wells were becoming dry. Because shaded drainages produced good standing crops of grasses, they were particularly utilized by cattle during wet periods (Fig. 3c). In the late-dry season (November–March), habitat use by all species was greatly

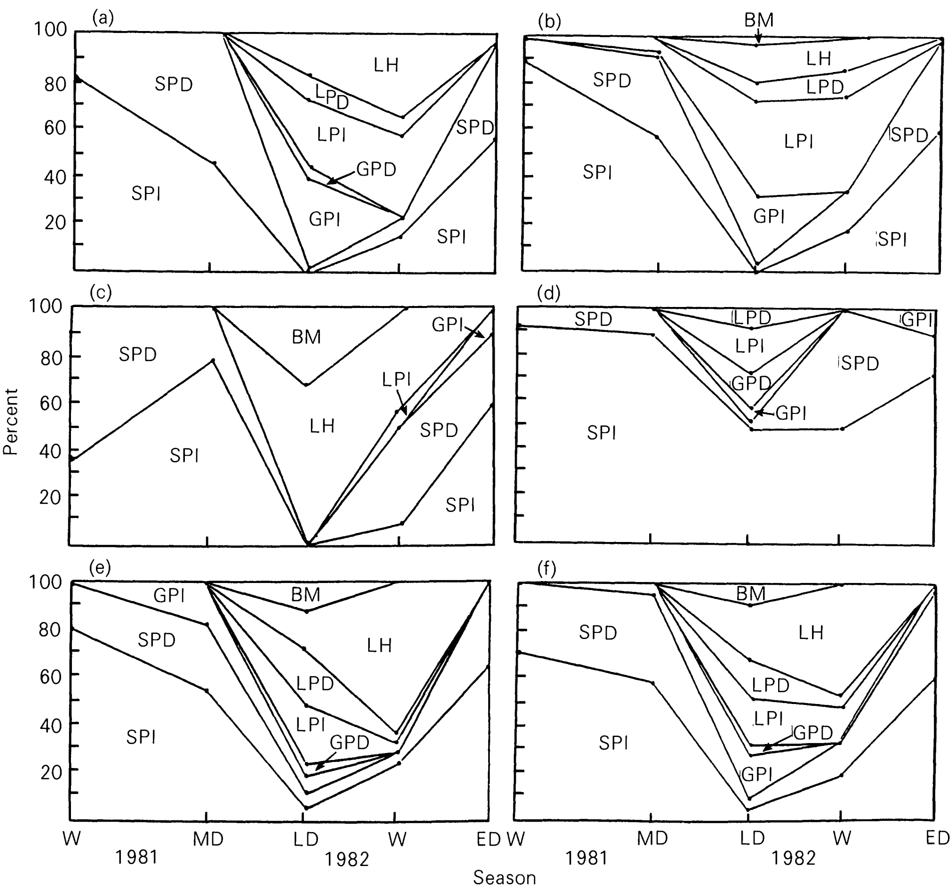

FIG. 3. Seasonal feeding use of various habitats (bite frequency basis) for (a) goats, (b) sheep, (c) cattle, (d) donkeys, (e) camels, and (f) the aggregate herd (excluding donkeys) in Ngisonyoka Turkana during 1981–82. Habitats are coded as SPI (sandy plains interdrainages), SPD (sandy plains drainages), GPI (gravel plains interdrainages), GPD (gravel plains drainages), LPI (lava plains interdrainages), LPD (lava plains drainages), LH (lava hills), and BM (basement-complex mountains). Seasons are coded as W (wet, April–May), ED (early dry, June–July), MD (mid-dry, August–October), and LD (late-dry, November–March).

diversified to include gravel sites near mountain footslopes, lava plains and hills, and the central mountains. The latter was again important for cattle because of higher quantities of grasses. Cattle appeared to be the most restricted species in the late-dry season, when they used only two habitats. The other species exploited an average of seven at this time. Considered for the aggregate herd (Fig. 3f), roughly 90% of all livestock feeding activity occurred in only three habitats during the wet through mid-dry periods. In contrast, six habitats received 90% of all feeding activity during the late-dry interval.

There appeared to be few major feeding constraints on habitat use for all species except cattle, which had to rely upon a rapidly diminishing supply of grass. Camels may have been slightly restricted because of their need to have access to mineral springs, but they could easily travel long distances (25–40 km round trip) to water (McCabe 1984; Coppock 1985). However, camels could not negotiate very rocky areas or steep (>40 °) slopes which were easily traversed by the other species. Sheep and goats seemed to have a lower capacity for travel compared with larger stock, and they were typically herded in heavily grazed areas closer to homesteads where they could feed more effectively than cattle or camels (Coppock 1985).

Seasonal patterns of niche segregation

Similarity values for diet composition and habitat use are shown in Fig. 4. Trends were better elucidated on a seasonal, rather than chronological, basis, and are displayed using a composited sequence from early wet through late-dry periods. The patterns of diet similarity depended upon the types of animals (grazer, browser, mixed feeders) compared.

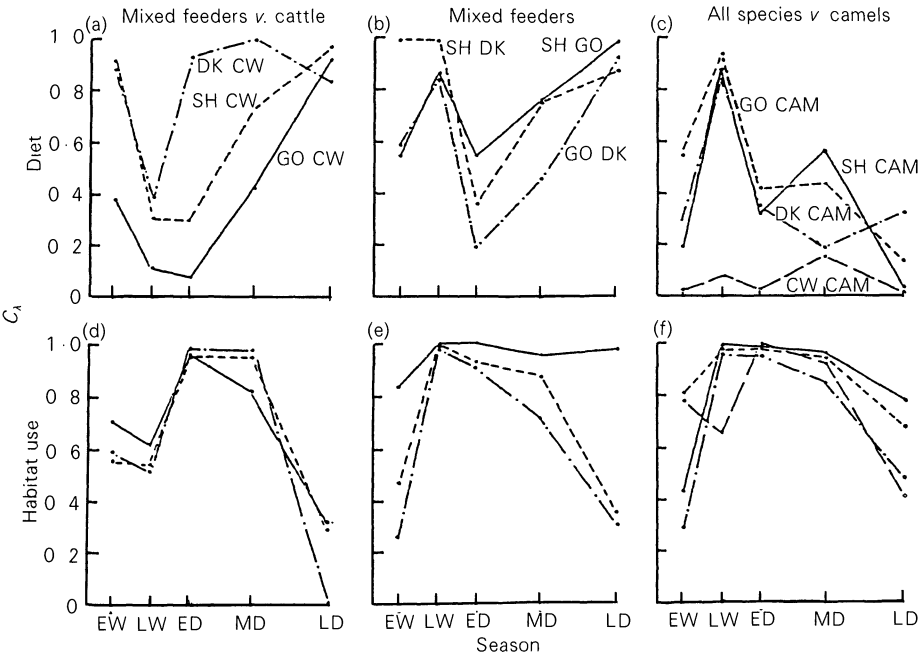

FIG. 4. Seasonal diet and habitat use similarity coefficients ($\hat{C}_\lambda$) between livestock species in Ngisonyoka Turkana during 1981–82. Coefficients potentially range from 0·0 (distinct) to 1·0 (complete similarity). Species are coded as GO (goat), SH (sheep), CW (cattle), DK (donkey) and CAM (camel). Seasons are coded as EW (early wet, April), LW (late-wet, May), ED (early dry, June–July), MD (mid-dry, August–October), and LD (late-dry, November–March).

Diet similarity between mixed feeders (goats, sheep, donkeys) and cattle tended to be lowest during late-wet and early-dry intervals when diets of the former included large quantities of non-herbaceous foods; similarity was highest during the late-dry when all consumed mostly grasses (Fig. 4a). Diet similarity among mixed feeders was lowest in the early-wet and early-dry intervals when rapid changes were occurring in the plant community (Fig. 4b). During these times goats exploited browse to a greater extent while sheep selected more green forbs among senesced grasses. Camels always had a very low diet similarity with cattle (Fig. 4c), and peak similarity between mixed feeders and camels in the late-wet period reflected high common use of dwarf shrubs. The late-dry season was a period of low diet similarity between camels and the other species because camels alone utilized more browse from tall trees. Diet similarity was generally low in the early-wet season when forage diversity dramatically increased and each species tended to use more distinct food items (Fig. 4a–c).

There was one seasonal pattern of habitat use similarity overall (Fig. 4d–f). During periods of greatest forage abundance (late-wet through mid-dry), similarity was high because of common use of sandy plains sites. During periods of forage scarcity (late-dry and early-wet transition) lower similarity was observed.

In terms of total resource utilization, i.e. of diet and habitat, the livestock differed most during the late-dry season. Nine of ten comparisons made in Fig. 4 showed less than 30% total similarity at this time. The high degree of segregation was most influenced by either diet (camels *v.* other species) or habitat use (cattle, donkeys, sheep/goats). In contrast, animals were the least segregated during the late-wet period, when six of the ten comparisons exceeded 80% total similarity.

DISCUSSION

Turkana livestock harvested a great variety of plants, and the forage-class compositions of diets were similar to those observed elsewhere for these species (Olsen & Hansen 1977; Pratt & Gwynne 1977; Mukasa-Mugerwa 1981; Schwartz & Ellis 1981; Migongo 1984). Larger stock tended to be more specialized feeders (Schwartz & Ellis 1981), and diet diversities declined for most species during periods of resource scarcity, which has also been noted previously (Jarman 1971; Vavra *et al.* 1977; Leuthold 1978). However, the increased diversity of camel diets during the dry season offset declines for the other species and contributed to a broad, temporally stable niche for the aggregate herd that resulted from a remarkably equitable use of vegetation. Mobility was also critical to exploit this heterogeneous landscape. Even during this year of 'good' rainfall and forage production, herds used sites throughout Ngisonyoka. Divergent patterns of habitat use were important in the spatial segregation of stock during periods of resource limitation. In sum, these livestock displayed a highly opportunistic and relatively efficient capacity for environmental exploitation. At the extremes, cattle enable the harvest of grass during years of 'average' or 'above-average' rainfall, while camels can harvest browse at all times. Camels are especially valuable during drought, when herbaceous production fails (McCabe 1984).

The complementary diets and spatial segregation of these animals is impressive and apears to mimic patterns observed for co-evolved communities of native ungulates (Jarman 1971; Leuthold 1978; Jarman & Sinclair 1979). However, despite superficial similarities, the major forces that shape community structure in pastoral or native systems are probably quite different. Long-term competitive interactions may play the key role in the latter, while patterns in Ngisonyoka could be more a fortuitous result of a diverse resource base in conjunction with ungulates that just happen to differ in food-selection tendencies. This is not to say that competition or natural selection is unimportant in Ngisonyoka; rather, it appears that such forces would be substantially mitigated by opportunistic management tactics.

Patterns of livestock feeding ecology in Ngisonyoka may not be generalizable to other pastoral systems because of local contingencies in resource availability and distribution. It is the heterogeneity in landscape and vegetation here that permits the maintenance of one of Africa's most diverse assemblages of livestock. For example, the broad trophic niche of the aggregate herd principally resulted from the distinct food habits and similar numbers of cattle and camels. Camel diets could have been redundant with those of cattle, given that camels can subsist on grass (Pratt & Gwynne 1977), yet Ngisonyoka offered camels a preferred alternative—namely, dwarf shrubs. Simply that both species are equally represented is unusual for Africa, as their distributions tend to be mutually exclusive because of different habitat requirements (de Montgolfier-Kouévi & Vlavonou 1981). Ngisonyoka is a good environment for camels because of the abundant browse and warm temperatures, but it is marginal for cattle because of the ephemeral nature of their grass supply. Without the wetter central mountains as a grazing 'refugium' during dry periods, cattle numbers would probably be markedly diminished over the long term (McCabe 1984). Another important contingency is the wide distribution of reliable watering points on the plains. With access to the seasonal flow of several large rivers and over sixty springs and hand-dug wells, the livestock can disperse and exploit residual patches of forage throughout the region, a factor that allowed herds to be segregated during periods of resource limitation. The tendency for consumers to aggregate, and not disperse, in dry periods as a consequence of centralized water distributions has been reported elsewhere in East Africa (Western 1975; Jarman & Sinclair 1979; Migongo 1984).

The mountains have another critical role as a catchment and distribution centre for rainfall (T. C. Hart *et al.* unpublished data). The concentration of run-off in drainages has facilitated the proliferation of woody vegetation on the plains, and the *Acacia* communities that accompany drainages produce most of the seeds and seedpods consumed by sheep and goats and provide shade that assists the establishment of otherwise uncommon grasses that were important for cattle (Coppock 1985). The value of drainages was evident from their high use; drainages were the most selected habitat type by the aggregate herd, with 31% of the feeding activity and a use-to-availability ratio of 6·2. In contrast, the sandy plains and lava hills were used roughly in proportion to availability, with ratios of 1·3 and 0·7, respectively, while the gravel plains (0·4), lava plains (0·4), and central mountains (0·3) were under-utilized during this year.

Economic development schemes in pastoral areas commonly result in reductions in the number of livestock species and restriction of movement, objectives that are obviously inimical to this traditional system (Coppock *et al.* 1985). The minimal unit of ecological viability may be the entire Ngisonyoka territory, as any subdivision, particularly if it excluded some groups from higher-elevation sites, would likely be disastrous for cattle production at the least. In addition, any declines in animal species diversity could greatly hinder food production. Coughenour *et al.* (1985) have estimated that the current system consists of over thirty important energy pathways that culminate in a wide distribution of milk, meat, and blood from camels (56% of total food energy), goats and sheep (24%), and cattle (18%). A typical development plan that emphasized cattle to the exclusion of other species would have to provide for an eventual replacement of over 80% of current food energy from non-pastoral imports and/or cattle and would literally waste a non-herbaceous resource that now provides nearly 65% of the forage energy to the system (Coughenour *et al.* 1985). Less radical tactics are recommended, both in terms of acceptability to the Ngisonyoka and with regard to the efficient use of this environment.

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