CHAPTER 10A

RELEVANCE OF KEY RESOURCE AREAS FOR LARGE-SCALE MOVEMENTS OF LIVESTOCK

PAUL SCHOLTE[#] AND JOOST BROUWER[##]

[#] NC-IUCN, Leiden University and Independent Consultant,
Nieuwe Teertuinen 12C, 1013 LV Amsterdam, The Netherlands
[##] Resource Ecology Group, Wageningen University, P.O. Box 47,
6700 AA Wageningen, The Netherlands
E-mail: scholkerst@cs.com

Abstract. Semi-arid rangelands show much spatial heterogeneity, with some parts producing more and better quality food for herbivores. The concepts of 'Key Resource' and 'Key Resource Area' have been developed to describe a resource that 'provides good-quality forage' and that 'reduces (inter-)annual variation in forage supply'. Illius and O'Connor (1999) formalised these concepts, arguing that in key resource areas herbivores experience a density-dependency relation with food resources, generally during the dry season. In other areas, generally during the wet season, non-equilibrium conditions govern the relation between herbivores and their food resources. They further argued that it is implicit that key resources show lower inter-annual variability than occurs on the (alternative) dry-season range, buffering livestock densities from climatic conditions. Key resource and outlying areas must further operate in a source–sink manner. In this chapter, we discuss the various assumptions and conclusions regarding key resources and key resource areas, using the floodplains of the Sahel, especially those of Waza-Logone in Cameroon, as examples. Sahelian floodplain grasslands are intensively exploited during the dry season, with cattle densities on a year-round basis about five times as high as in surrounding drylands. We come to the conclusion that the inter-annual variability in the *quantity* of the forage production of the Sahelian floodplains is not less, but often greater than that of surrounding areas. Forage *quality*, however, may be more constant. The model of Illius and O'Connor would be more realistic if it included intra-annual variability in forage availability, variability in accessibility of that forage, and associated differences therein between the dry-season range and the wet-season range. The importance of a resource varies from year to year, depending among other things on inter-annual variability in rainfall in the wet-season grazing range and in (the catchment upstream of) the dry-season grazing range. When it is of great importance, it may be considered a 'key resource', but in another context the same resource is not necessarily a key resource. Because of this spatial and temporal variability in rainfall and forage availability, there is no unequivocal source–sink relationship between the Sahelian floodplains and the associated wet-season grazing ranges. Forage in a key resource area does not necessarily provide the only key resource in the grazing system. Water, for instance, can be important as well. We end by discussing what our findings mean for the key resource area concept of Illius and O'Connor, and by presenting a new definition of key resource area which is also relevant to other trophic systems.
Keywords. floodplain; key resource area; livestock; population control; Sahel

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INTRODUCTION

Semi-arid rangelands form the habitat of many large herbivores, and have been the domain of cattle herders for hundreds of years (e.g., Prins 2000). Spatial heterogeneity in these semi-arid rangelands has been attracting the attention of ecologists for about half a century (Macfadyan 1950; Coughenour 1989; Hary et al. 1996). Some of the most distinctive features associated with this heterogeneity are drainage lines and wetlands and their accompanying vegetation. Examples are *Acacia* woodlands along dry rivers in Eastern Africa (Wuant and Ellis 1990), wet 'dambo' depressions in Southern Africa (Scoones 1995), and seasonally flooded grasslands in Sahelian Africa (Hiernaux and Diarra 1983; Howell 1988). At such features, water and nutrients are concentrated, primary and secondary production potential are greater, and production risk is often less than in the surrounding rangelands. Higher-altitude areas, with associated higher rainfall and more humid vegetation, may also constitute a distinctive feature in otherwise arid and semi-arid regions (Prins and Loth 1988; Hary et al. 1996). Because of the temporal heterogeneity found in semi-arid areas, in particular seasonal and inter-annual periods of drought, this spatial heterogeneity can be crucial for the survival of local herbivores. It allows herbivores to alternate between food sources (Drent and Prins 1987), according to their needs and the time of year. To this purpose long-distance migrations are often undertaken, by wild as well as domestic herbivores (Breman and De Wit 1983).

Spatial heterogeneity in (semi-)arid regions can be crucial for the survival of herbivores as they migrate

Herbivores shift to these high-production areas because they provide so-called 'Key Resources' (Scoones 1995). The term 'Key Resource' has been applied in a range of disciplines, varying from management science to anthropology and ecology, to stress the importance of a relatively limited resource for the survival of an individual or a population. In rangeland science, key resources have been mentioned since the early 1990s, although often in passing only, to stress their importance for the survival of herbivore populations during prolonged dry seasons (Drent and Prins 1987; Bayer and Waters-Bayer 1994; Scoones 1994; 1995; Hary et al. 1996). In relation to herbivores, two characteristics of key resources have received particular attention: they provide "good quality forage" and they "reduce (inter-)annual variation in forage supply" (Bayer and Waters-Bayer 1994). No reference is made to the minimum quantity of forage production, however.

'Key resource' has been applied in a range of disciplines to stress the importance of a limited resource for survival of individuals or populations

Until now the use of the term key resource seems to have been limited to forage resources, excluding other factors that may also be crucial to the survival of herbivores. In the African Sahel, for instance, as in most semi-arid areas, grazing patterns depend essentially on water availability. Dry-season grazing of cattle, but also of most wild herbivores, generally occurs within a distance of 20 km of sources of water (e.g., Le Houerou 1989; Fryxell and Sinclair 1988).

The term ‘Key Resource Areas’ was conceptualised by Illius and O’Connor (1999). They formalised the distinction between key resource-producing areas, where herbivores experience a density-dependency relation with food resources, generally during the dry season, and areas where non-equilibrium conditions are dominant, mostly in the herbivores’ wet-season ranges (Box 10.1). In key resource areas, animals should further have a sufficient impact on the vegetation to experience intraspecific competition. Illius and O’Connor (1999, 2000) further argued that “it is implicit that these resources show lower inter-annual variability than occurs on dry-season range”, buffering livestock densities from climatic conditions. Key resource and outlying areas must further operate in a source–sink manner, with key resource areas maintaining by definition a higher level of herbivory in outlying areas than these could support on their own (Illius and O’Connor 1999).

Box 10.1. *Historical development of the ‘Key Resource Area’ concept*

A central concept in range ecology is carrying capacity. Herbivore numbers are controlled by the availability of forage, and the availability of forage is controlled by animal numbers. This pattern of negative feedback eventually produces a stable equilibrium between animal and plant populations (Behnke and Scoones 1993). This equilibrium concept was largely based on the then reigning Clementsonian climax model of vegetation change. Its inadequacy in especially rangelands dominated by annual grasses was highlighted for arid Australia in the early 1980s (e.g., Westoby 1980). For such circumstances the alternative ‘state and transition’ model was postulated, which contested simple linear vegetation change (Westoby et al. 1989). Increasingly based also on examples from Africa, it is argued that plant production in highly variable climates is largely determined by rainfall and unaffected by herbivore population densities (e.g., Ellis and Swift 1988). The new paradigm of ‘Rangeland at Disequilibrium’ came to the fore in the early 1990s, and challenged the prevailing rangeland management practices (Behnke et al. 1993; Scoones 1995). In a reaction to this, Illius and O’Connor (1999) developed a somewhat different view of African rangeland functions. They argued that (1) herbivore numbers are regulated in a density-dependent manner by the limited forage available in so-called ‘Key Resource Areas’, utilised during the dry season mainly; (2) strong equilibrium forces exist over this limited part of the grazing system, while the animal population is virtually uncoupled from resources elsewhere in the system; (3) the wet-season grazing range is more heavily utilised by animal populations sustained by key resource areas than would apply in the absence of the key resource areas; and (4) the uncoupling of the animal population from the wet-season grazing range vegetation, in systems containing a key resource area, carries the risk of increased degradation of vegetation resources in the wet-season grazing range. In addition, they assumed in their associated modelling study (Illius and O’Connor 2000), that (a) potential primary production in the key resource area is dependent on rainfall only and was therefore the same in the key resource area as in the remainder of the grazing system; and (b) rainfall in the key resource area and in the remainder of the grazing system varies synchronously, but with a lower Coefficient of Variation (CV) in the key resource area than in the remainder of the grazing system. This was achieved by setting the deviation from mean annual rainfall in the key resource area in a particular year at a fraction of the deviation from mean annual rainfall in the remainder of the grazing system. Illius and O’Connor also looked at (c) different area ratios between key resource areas and wet-season grazing ranges. The greater that ratio, the greater the positive effect of the key resource area on livestock numbers.

Table 10.1A. *Cattle densities in Sahelian seasonally flooded grasslands*

	Waza-Logone (Scholte et al. 2006)	**Logone Floodplain** (Schrader 1986)	**Chad, Lake Fitri** (DHV/Labo 1994)	**Mali, Inner Delta** (Wilson et al. 1983)		**Floodplains theoretical** (De Bie 1991)
Period	Entire dry season 1993-99	Dry season March–June 1985 drought	Feb. 1993	Flooding season Oct 1980	Dry season Febr. 1980 / March 1981	
Area (km^2)	500	± 740	1,600	11,400		
Cattle (km^2)						
during obs. period	27 → 69[1]	30[2]	61[3]	10	75/78	80-137[4]
on 12-month basis	13 → 34		31			
Calculated min. number of cattle involved [5]	*34,000*	*22,000*	*98,000*	*114,000*	*890,000*	

1. Cattle pressure recalculated to average density during the six months that the floodplain is accessible to livestock (see text); does not take into account sedentary herds
2. Including sedentary herds (approximately 10% of total)
3. Half of the surveyed Fitri area has a density lower than 5 cattle km^{-2}, i.e., open water or land far from the lake, motivating the presented doubling of the recorded densities
4. Based on theoretical calculations, considering soils with high nutrient status. Recalculated to average densities over 6 months as under 1
5. Indicated to appreciate the importance of the area; does not take into account differences in peak densities and averaged densities.

In relation to the concept of ‘Key Resource Areas’, the seasonally flooded grasslands, or ‘floodplains’, of the African Sahel deserve further investigation. These grasslands are intensively exploited during the dry season, with livestock densities up to 60-100 cattle km^{-2}, ten times as high as cattle densities in dry-season ranges at the same time of the year. On a year-round basis, cattle density on floodplains is only about 3-6 times as high as in surrounding drylands, because high water levels make the floodplains inaccessible to cattle for up to six months each year (compare Tables 10.1A and 10.1B). Box 10.2 provides a brief general description of the seasonally flooded grasslands of the Sahel.

This important concentration of livestock motivates the consideration of these large seasonally flooded grasslands as key resource areas. But do they behave according to the above-cited properties? Are they really ‘Key Resource Areas’ *sensu* Illius and O’Connor (1999)? Should key resource areas perhaps be defined slightly differently? Or should different types of key resource areas be recognised? We address these matters by discussing the following questions. The examples used to illustrate that discussion mostly come from the Waza-Logone Floodplains grazing system, of which details are provided in Box 10.2 and Box 10.3.

***Table 10.1B**. Cattle densities in Sahelian wet and dry season ranges (drylands)*

	Chad Basin				**Niger Basin**							**Theoretical** (De Bie 1991)[2]
	Chad, Centre (DHV/Labo 1994)		Nigeria / Borno (ERGO 1990)[1]		Mali, Inner Niger Delta (Milligan et al. 1982)[1]		Mali, Gourma (Milligan 1983; RIM 1985)		Niger, SW (Milligan 1982)			
Rainfall (mm yr^{-1})	150-550	150-800	400-800		400-600		300-500		200-500			200-800
Season	rainy	dry	rainy	dry	early dry	late dry	late rainy	dry	late rainy	early dry	dry	year-round average
Large wetlands	yes		yes		yes		no		no			
Area (km^{-2})	60,000	117,000	117,000		36,000		81,000		81,600			
Cattle (km^{-2})	10.1	7.8	21.4	25.3	22.5	22.5	5.7	4.3	4.1	4.6	3.5	
TLU (km^{-2})	9.5	7.1	21	23.2			5.6	4.3	5.9	6.6	5.0	8-16
Calculated min. number of cattle involved[3]	*600,000*	*910,000*	*2,500,000*	*2,960,000*	*810,000*	*810,000*	*460,000*	*350,000*	*335,000*	*375,000*	*285,000*	

[1] High (peak) density because of the proximity of floodplains
[2] Based on theoretical calculations, considering soils with low nutrient status
[3] Indicated to appreciate the importance of the area; does not take into account differences in peak densities and averaged densities.

Temporal variability

- Is the inter-annual variability in food production of the Sahelian floodplains less than that of alternative dry-season grazing lands?
- Does the food production of the dry-season ranges vary in synchrony with that of the wet-season ranges, and is it important whether it does?
- Does the role of Sahelian floodplains in the associated grazing systems vary between wet years, normal years and dry years?

Spatial variability and density dependence

- Do Sahelian floodplains offer better-quality food in greater quantity than do alternative dry-season ranges?
- Do the Sahelian floodplains regulate, in a density-dependent way, the number of livestock grazing the associated wet-season dryland grazing areas?
- Related to that, do the Sahelian floodplains act as a source for livestock numbers, and the wet-season grazing areas (that is, the dryland) as a sink?
- Further: does the presence of the Sahelian floodplains occasionally lead to an increased degradation of the wet-season grazing range?

Other assumptions by Illius and O'Connor (2000)

- Does it matter whether the potential primary production in a key resource area, on a per-hectare basis, is assumed to be the same as in the associated wet-season grazing area?
- Does it matter whether plant growth in dry-season grazing areas, or key resource areas, is assumed to vary in synchrony with plant growth in wet-season grazing areas?
- Does it matter whether dry season and wet season are both set at six months of the year, instead of another ratio?
- Are potential effects of key resource areas on surrounding wet-season grazing areas, including on species composition, perhaps related to food accessibility as much as to food availability?

Additional aspects

- Would the effects of a number of small key resource areas forming one grazing unit, such as a number of adjacent isolated wetlands, differ from the effects of one large key resource area?
- Does it matter whether, in relation to key resource areas, the focus is so generally on food instead of on water or some other factor?
- The above questions implicate that herbivore production is increased by the presence of key resource areas, but does this also hold for the individual animals?

We end by discussing what our findings mean for the key resource area ideas of Illius and O'Connor and by presenting a new definition of key resource area which is also relevant to other trophic systems.

Box 10.2. *African seasonally flooded grasslands and their utilisation by pastoralists*

Flooding and primary production

The major African floodplains are associated with rivers that have strong seasonal differences in volume (Denny 1993). These include the Zambezi, Nile and Niger Rivers, as well as the rivers flowing into Lake Chad and their tributaries (Figure 10.1). Spilling of the river water over the levees onto the associated floodplains can take place from once to several times a year. The regularity of flooding and its depth and duration obviously influence what plant, and animal, species are present (Denny 1993).

Maximum flood depth also determines aboveground biomass production of perennial-grass communities in African seasonally flooded grasslands (Scholte 2005). Under deeply inundated circumstances, i.e., 2-3 m, aboveground standing herbaceous biomass may reach 30 tons DM/ha (Hiernaux and Diarra 1983), up to ten times as high as in surrounding dryland areas (Le Houerou 1989; Prins 1996). The forage quality on floodplains, when characterised by its protein content, is generally negatively correlated with aboveground biomass. At the end of the flooding season, these floodplains are covered with a large quantity of grasses of below maintenance quality (Breman and De Wit 1983; Hiernaux and Diarra 1983; Howell et al. 1988; Prins and Olff 1998; Olff et al. 2002). The main grazing asset of the seasonally flooded grasslands is regrowth, which is of much higher quality. This regrowth is triggered by burning and grazing, and gradually becomes available during the dry season (Hiernaux and Diarra 1983; Howell et al. 1988; Scholte 2005). On the Inner Niger Delta floodplains in Mali, regrowth biomass was found to be a linear function of previous aboveground biomass (Breman and De Ridder 1991), and thus indirectly a function of maximum depth of the preceding flood. Regrowth assessments in Logone, Cameroon, suggest a regrowth production threshold at ±50-100cm maximum flood depth, corresponding to an aboveground biomass of ±10 tons DM ha^{-1}. With a lower flood depth hardly any regrowth is produced because of the lack of moisture stored in the soil in those parts of the landscape (Scholte 2005).

Pastoral exploitation

Similar to most other seasonally flooded grasslands, the almost featureless floodplains of Mali's Inner Niger Delta, the Sudd (Sudan) and the Lake Chad wetlands are home to more than a million cattle when the floods have receded. The same can be said of the floodplains of the Zambezi, and of other major rivers in those regions of Africa where disease does not preclude the grazing of, in particular, cattle. The herders let their cattle graze these floodplains in a complicated system established over perhaps centuries, with various traditional rights of grazing, passage, water access and management, now threatened by a host of new developments. By and large the herders use the floodplains when they can, i.e., once the floods have receded and there is sufficient grass and herb growth of sufficient quality available. Water availability generally does not pose problems. Labour needed to water animals is an important factor in the selection of areas (i.e., floodplains), yet production is generally not influenced by this factor. As mentioned above, good-quality regrowth can be triggered by setting fire to the old, poor quality growth (e.g., Van de Vijver 1999; Van de Vijver et al. 1999; Van Langevelde et al. 2003). When access to the floodplains becomes impossible, for example, because of the lack of water or because of the availability of better forage in the surrounding dryland areas, the herders move their cattle to those uplands. How and when this happens depends on, among other things, the timing of the flooding of the river plains relative to the falling of the rains in the drylands.

TEMPORAL VARIABILITY

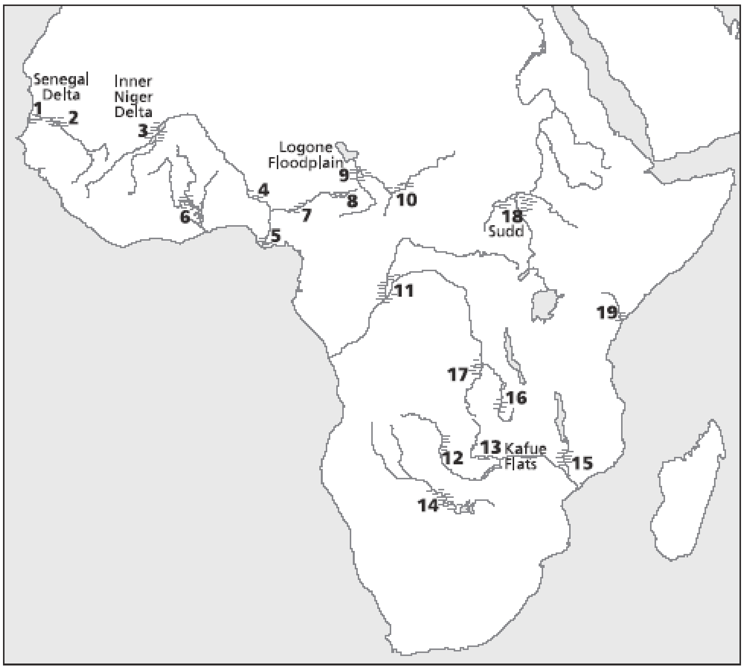
Is the inter-annual variability in food production of the Sahelian floodplains less than that of the wet-season range?

Relatively low inter-annual variability in food production is considered to be an important characteristic of key resource areas (Illius and O'Connor 1999, 2000). Key resource areas may depend on groundwater, infiltrated surface water or permanently available surface water to buffer them against rainfall variation and maintain high production levels with relatively low inter-annual variability. Examples include the afore-mentioned small, ephemeral drainage lines (Scholte 1992), (semi-)permanent drainage lines (Wuant and Ellis 1990), lake shores (Loth and Prins 1986; Prins 1996), and higher-elevation areas with higher rainfall than the surrounding (semi-)arid lowland areas (Hary et al. 1996). Such areas occur in the Sahel (Le Houerou 1989) as well as in Eastern Africa (Prins and Loth 1988). In all these cases local hydrological processes appear to dominate the concentration of water in the key resource area, leading to greater hydrological and production security than in the surrounding drylands. But need this always be the case?

Water resources in floodplains are a combination of local rainfall and flooding. In the Lake Chad basin the discharge of feeding rivers is responsible for 50% (Waza-Logone floodplains) to more than 90% (Lake Chad itself) of the volume of the water resources (Naah 1992; Olivry et al. 1996). The Coefficient of Variation (CV) of the annual discharges of these rivers range from 26 to 98%, higher than the CV of annual rainfall of 26-43% in surrounding Dry-Season Ranges (Table 10.2). The situation in the Inner Niger Delta floodplain (Mali) is quite similar (Table 10.2). Inter-annual variability in the extent of the area inundated is greater still, sometimes more than 100%.

Inter-annual variability in food quantity of the Sahelian floodplains is not less than that of the wet-season range

There are a number of reasons for this large variability in river discharge and extent of flooding. (1) Not all rainfall events cause run-off and an increase in river flow. Only rainfall events above a certain intensity and duration threshold will do so, and the occurrence of such extreme events is more variable than annual rainfall. Run-off and river flow are also influenced by the distribution of rainfall through the rainy season, which again is more variable than annual rainfall totals. (2) Topography of the floodplains also influences the extent of flooding. If a certain flood level is reached, a whole new basin may be flooded, which would not have happened if the flood level had remained fractionally lower. This, too, can lead to an increase in the variability of the extent of flooding. (3) Human intervention of course also has an effect. Within a floodplain humans may try to influence the flooding of certain areas to further pastoral, agricultural or fishing aims. At a higher scale, through the operation of dams, a more or less constant, large volume of river flow is diverted or lost to evaporation each year. This reduces the average flow downstream, but the absolute variations, and thus the standard deviation, of the flow are influenced less. As the CV equals the standard deviation divided by the mean, regular annual water takeoffs via dams increase the CV.



No and name	Country	Area at peak flood (km^2)	Floodplain type
1 Senegal Delta	Senegal	8 000	Coastal delta
2 Senegal Valley	Senegal	5 000	Fringing floodplain
3 Inner Niger Delta	Mali	30 000	Internal delta
4 Niger fringing plains	Nigeria	5 000	Fringing floodplain
5 Niger Delta	Nigeria	36 000	Coastal delta
6 Volta River	Ghana	8 500	Fringing floodplain
7 Benoué River	Nigeria	3 100	Fringing floodplain
8 Benoué River	Cameroon	1 000	Fringing floodplain
9 Logone Floodplain	Cameroon	5 000	Fringing floodplain
10 Chari and Logone	Chad	63 000	Fringing floodplain
11 Congo River	Congo	?	Fringing floodplain
12 Barotse plain	Zambia	10 750	Fringing floodplain
13 Kafue Flats	Zambia	4 300	Fringing floodplain
14 Okavango	Botswana	17 000	Internal delta
15 Shire River	Malawi	1 000	Fringing floodplain
16 Kifakula Depression	Congo	1 500	Fringing floodplain
17 Kamulondo	Congo	12 000	Fringing floodplain
18 Sudd	Sudan	92 000	Fringing floodplain
19 Tana Delta	Kenya	1000	Coastal delta

Adapted from Drijver and Marchand 1986 and Welcomme 1979.

Figure 10.1. *The location of large (> 1000 km^2) seasonally flooded grasslands in Africa (Scholte 2005)*

Furthermore, the major floodplains in the African Sahel (Figure 10.1) are surrounded by medium-rainfall areas, with higher-rainfall areas located 100-500 km to the south. Rainfall CV decreases from an average 26% in the medium-rainfall areas to an average of less than 18% in the high-rainfall areas (Table 10.2). The forage quantity is relatively moderate in the medium-rainfall areas and high in the high-rainfall areas. Forage quality is generally low throughout, with exception of browse and regrowth in generally scarce lower-lying areas (Breman and De Wit 1983; Le Houerou 1989). On the floodplains themselves, forage production quantity is generally high, and quality varies (not so high immediately after flooding, high following burning and regrowth).

Table 10.2. *Coefficients of variation of key parameters of wet- and dry-season ranges, including key resource areas (KRA) in the African Sahel*

		Area	Average rainfall (mm yr^{-1})	Rainfall CV (%)	CV (%) rainfall in main catchment areas	CV (%) Flood level[2]
NORTH ↔ SOUTH	Wet-season range	North Sahel	55	81[1]		
			153	43[1]		
	KRA flood plains	Lake Chad	284-(576)	(26)-43	11-26	35 Chari River discharge 51 Lake levels[3]
		Inner Niger Delta (Mali)	300-600	30	17-26	55 Water level Niger river 108 Area of Inner Niger Delta inundated
		Lake Fitri (Chad)	394	30	26-30	98[4] Batha River discharge at Ati
		Waza-Logone (Cameroon)	576	26	11-14	26 Logone River[5] 39 Secondary sources [6]
	Dry-season range	South Sahel (Ndjamena, Chad)	576	26		
	High-rainfall areas, Cameroon	Maroua	806	18		
		Guider	919	16		
		Garoua	972	16		
		Ngoundéré	1513	11		

[1] Lack of reliable rainfall data available, based on data set of, respectively, 11 and 9 stations in the Sahel (Le Houerou 1989)
[2] Maximum river discharge was considered the best available parameter to predict flooding levels in the Logone floodplain and Lake Chad (see Naah 1992; Mott Macdonald 1999), Inner Delta, both flood level and flooding area (Quensiere 1994; Zwarts 2002; Zwarts pers.comm.)
[3] Quasi-linearly correlated with surface area of lake (Olivry 1996). Data set does not include the dry 1980s, CV thus underestimated
[4] Total annual discharge volume, based on 1955-1989 data set only
[5] Based on 1933/1948–1997 data set
[6] Based on data set of 1970 and 1980s.

Box 10.3. *Pastoralist responses to inter-annual variability in Sahelian floodplains: two examples from Waza-Logone*

The key resource area characteristics described in Box 10.2 for Sahelian floodplains show that the discussion on population size regulation by density-dependent factors or by density-independent factors should not ignore inter-annual variability. We give here two examples of such variability for the Waza-Logone Floodplains during a period of six wet years (1993-1999) and during a severe drought (1985), to show the implications of this inter-annual variability for the exploitation of the available grazing resources by cattle.

1. Effects of reflooding of part of a floodplain previously dammed out

In 1993, the Waza-Logone project initiated a pilot reflooding by breaching an embankment that had closed off a small branch of the Logone river, triggering the annual reflooding of a downstream area of ±180 km^2 (Scholte et al. 2000; Scholte 2005). From 1993 till 1999, the project monitored the impact of this reflooding, thus imitating a period of six wet years following a prolonged period of dry years. Such a sequence was not exceptional during the last century.

During the study period, annual grasses were replaced by rhizomatous grasses, with an annual conversion rate of 7-10% of the 180 km^2 reflooded area (Scholte et al. 2000). Here, as well as in an additional area of ± 500 km^2, the maximum flood level was raised by about 20 cm, leading to a ±30% increase in aboveground biomass (Box 10.2). We monitored nomadic pastoralists' responses to these changes through interviews about their migration patterns in the reflooded area (Scholte et al. 2005; Scholte 2005). Grazing intensity of nomadic herds, expressed as cattle density averaged over the six months of dry season, increased 2.6-fold from 1993 till 1999 (Figure 10.2). In the first year, the increase in grazing pressure was caused by a longer stay of herds already present (Figure 10.3). In later years the reflooded area experienced especially an inflow of herds and herders.

The assumption that the monitored reflooding imitated a period of six wet years holds especially for the floodplain vegetation. As indicated, with a lag of one year annual grasses started to be replaced by perennial grasses, generally spreading from rhizomes. Contraction and expansion of rhizomatous grasses are normal phenomena during periods of long-term climatic and annual rainfall fluctuations. Flood depth – aboveground biomass relations also showed a lag in the full response, with the 1996 production per unit of flood depth higher than in 1994, the first year of reflooding.

The reaction of the pastoralists was influenced by developments elsewhere in the floodplain, or lack thereof. In the remainder of the floodplain, rainfall and flooding during the 1993-1999 study period were rather average, and thus not similar to 'wet years' as in the reflooded area. Most of the increase in pastoral camps was caused by the arrival of pastoralists from elsewhere in the floodplain, pulled in by the increasing availability of forage resources in the reflooded floodplain. In case of more widespread favourable rainfall and flooding conditions, they would have stayed where they were elsewhere in the floodplain. In addition, a small group of pastoralists had changed their migration completely and entered the Logone floodplain for the first time since years, settling in the reflooded area immediately following the reinstatement of flooding. The relative grazing pressure in the reflooded zone, compared to the entire floodplain, therefore increased till 1996 but subsequently stabilised, suggesting a saturation in cattle density in the reflooded zone after three 'wet years'.

Pastoralists' responses to floodplain rehabilitation were in line with the Ideal Free Distribution model, with any increase in forage production subject of increased consumption (Scholte et al. 2005; Scholte 2005). No overshoot in number of pastoralists and cattle has taken place. Initially feared for, such overshoot would have had an impact on perennial vegetation that however continued to expand during the study period. Nor were there any signs of territorial blocking of newcomers, except for the first-year delay in responses (Figure 10.2). Cattle herds should further be considered as one (meta-)population, with regular exchanges, resulting in rather uniform productivity levels.

(cont.)

Box 10.3. (cont.)

2. Dynamics during a period of drought

In the years 1983-1985, on the other hand, the entire Sahel experienced a period of severe drought. Rather strikingly, the 1985 cattle densities in the Waza-Logone floodplain, following the drought and six years after the cessation of annual flooding of parts of the floodplain, were very comparable to the densities prior to the reflooding in 1993, a year with rather average rainfall and flooding (Table 10.1A). The origin of the migrating cattle, however, was completely different. During the dry season in the drought year 1985 those pastoralists normally present in the floodplain had migrated further south into high-rainfall areas (Table 10.1A). Pastoralists present in the floodplain in 1985 came from further north, and had changed their migration, which used to be directed into the Lake Chad bed (Schrader 1986; Clanet 1996). Lake Chad flood sources show a higher CV in their annual discharge than the flood sources of the Waza-Logone floodplain (Table 10.2). At least in 1985, the Lake Chad grazing resources were apparently less dependable than those of the Waza-Logone floodplain. In the same year 1985, cattle losses due to diseases and exhaustion in the Waza-Logone floodplain were much higher than those recorded in 1997, estimated at, respectively, 10 and 0.9% of the total number present.

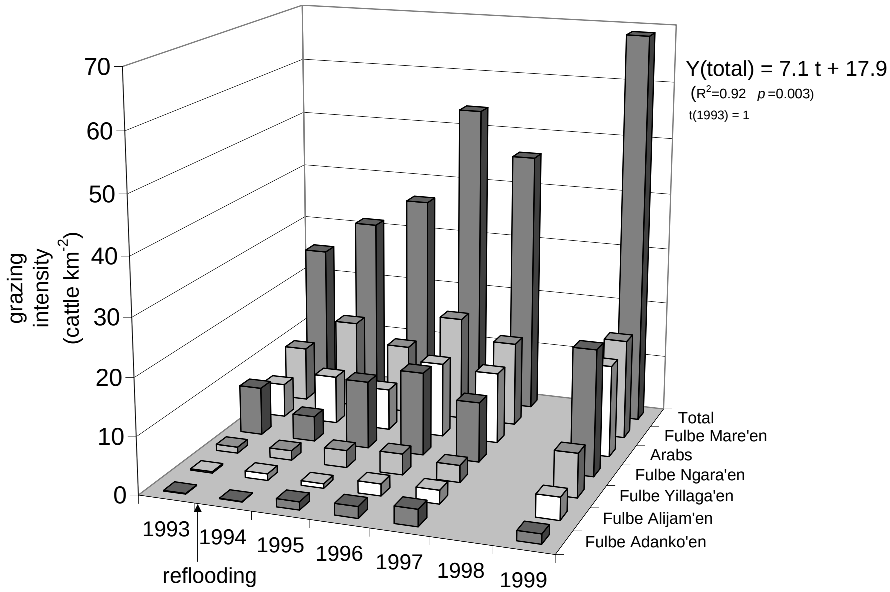


Figure 10.2. *Linear increase in grazing intensity, averaged over a dry season of 6 months, following reinstatement of old annual flooding regime and gradual recovery of the grassland vegetation in the Waza-Logone Key Resource Area (1993-1999). Cattle density given for each of the six pastoral clans and as total*

Based on the preceding we conclude that the inter-annual variability in the *quantity* of the food production of the Sahelian floodplains is not less, but often greater than than that of surrounding medium-rainfall areas. This does, however, not necessarily hold for the inter-annual variability in the *quality* of the food production of the Sahelian floodplains. Data on the inter-annual variation in food quality are, however, near-absent from the literature.

Does the forage production of the dry-season ranges vary in synchrony with that of the wet-season ranges, and is it important whether it does?

Illius and O'Connor (2000) only looked at total annual forage production during a year, not at intra-annual variation in forage availability. They then modelled three situations, with either no, partial or complete restriction in the seasonal accessibility of the two range areas. They assumed that the quality of dead forage biomass was equivalent to the quality of living forage biomass. Thus they excluded intra-annual temporal variability in forage availability from their modelling, and also differences between the wet-season range and the dry-season range in that intra-annual temporal variability in forage availability.

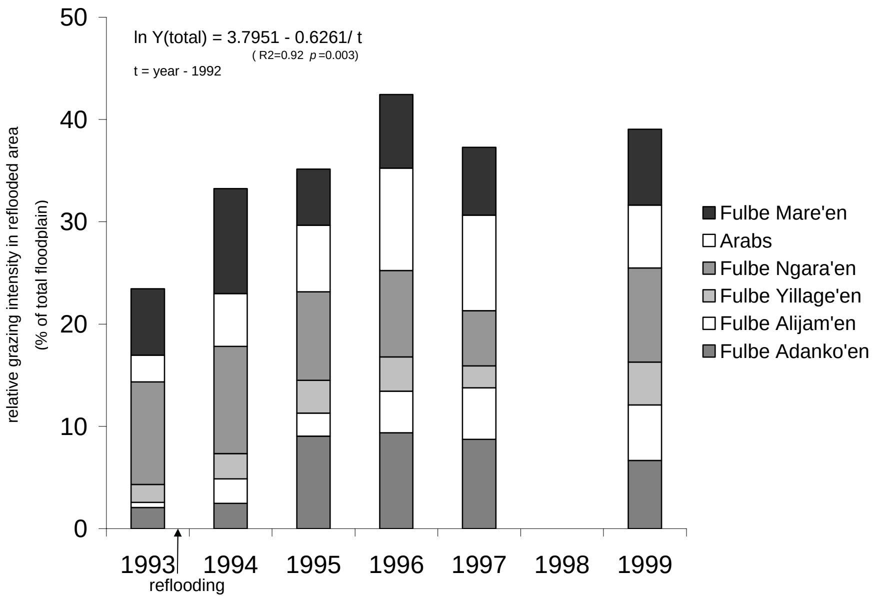


Figure 10.3. *Changes in grazing time by the six pastoral clans spent in the reflooding impact zone, as a percentage of the grazing time they spent in the Waza-Logone floodplain as a whole during each six-month dry season (Note that the y-axis scale refers to the totals for the six clans together, and not to contributions by individual clans)*

Whether forage production of the dry-season ranges varies in synchrony with that of the wet-season range will depend on where the dry-season range, in our case consisting of floodplains, gets its water from for primary production. If flooding is from local rainfall, then forage production will vary more or less in synchrony with wet-season ranges. If the flooding is caused by rainfall far away, then there will often be a delay in forage production on the floodplains compared to the surrounding drylands. Moreover, the storage of water in the soil during flooding allows primary production to resume following grazing or burning, long after the rains, and the flooding, have ceased. Primary production in the Okavango Delta (Botswana), for example, is nearly completely out of phase with that of the surrounding drylands.

What is also important, however, is the *accessibility* of the forage produced. In the wet-season ranges, there may still be some forage left during the early part of the dry season, but the drying-up of surface water for drinking can make it inaccessible to large grazers. Construction of permanent water points can make such forage more accessible, but during poor-rainfall years it can also increase the danger of overgrazing (Le Houerou 1989). In the floodplains of the dry-season range, on the other hand, the flooding that causes the forage to be produced can also limit the accessibility of that forage. What is important to the grazing system is not only that the floodplains produce more or better forage than the wet-season range, but that the forage is accessible to the grazers at a time when food left on the wet-season range is not accessible.

Including intra-annual temporal variability in forage availability and differences therein between the dry-season range and the wet-season range, would make the model of Illius and O'Connor more realistic. It would also show that the dry-season key resource area does not necessarily provide the only key resource in the grazing system (see the proposed new definition of a key resource at the end of this chapter).

Does the role of Sahelian floodplains in the associated grazing systems vary between wet years, normal years and dry years?

Illius and O'Connor did not look into this, but the role of the Sahelian floodplains certainly varies between years (Box 10.3). Again, this shows how the importance of the floodplains in a particular year depends on the circumstances that year in both the floodplains and the associated drylands. In other words, a key resource area does not fulfil a key role independently of its spatial or temporal context.

SPATIAL VARIABILITY AND DENSITY DEPENDENCE

Do Sahelian floodplains offer better quality food in greater quantity than does the wet season range?

Illius and O'Connor (2000) assume that the quality of the food in wet- and dry-season ranges is the same. They also assume that, during below-average rainfall years, rainfall and forage quantity are always better in the key resource area, i.e., the floodplain. By and large it depends on the time of year whether Sahelian floodplains offer better-quality food in greater quantity than do alternative dry-season ranges, also in below-average rainfall years. See Box 10.2, and the answers to the first two questions above.

Do the Sahelian floodplains regulate, in a density-dependent way, the number of livestock grazing the associated wet-season dryland grazing areas?

The concept of key resource areas, with their density-dependent effects on the associated herbivore populations, implies a coupling of the population dynamics to the key resource area's vegetation, at least during periods of drought (Illius and O'Connor 1999). Increased grazing intensity and intraspecific competition on high-quality forage did indeed take place during several years in the Logone floodplain. During such years pastoralists generally adjusted the length of stay in the floodplain based on the availability of forage sources (Figure 10.3).

However, in none of the relatively well-studied major seasonally flooded grasslands in Africa, an inter-annual impact of grazing on the vegetation was reported, not even after severe droughts (Ellenbroek 1987; Hiernaux and Diarra 1983; Howell et al. 1988; Scholte et al. 2000). Degradation of soil and vegetation was, however, reported from surrounding dryland grazing ranges (Howell et al. 1988). Characteristics that explain the resilience of the seasonally flooded grasslands include the high belowground biomass (±70% of total biomass) that is inaccessible to grazing animals because of the firm vertisols and the six months of seasonal protection due to rainfall pounding and subsequent flooding. Drent and Prins (1987) also argued that, because the herbivore is prisoner of its food supply, vegetation under 'natural conditions' is free from disturbance due to the herbivore. Ideal free distribution, observed in at least one Sahelian Floodplain (Box 10.3; Scholte 2005; Scholte et al. 2006) is certainly one of the mechanisms that make it rather unlikely that herbivores exercise long-term disturbance.

The floodplains are protected from lasting damage from overgrazing by their annual flooding. This makes it likely that herbivore numbers are controlled in these areas but not (density-dependent) regulated. The drylands directly surrounding the floodplains are not flooded, and the vegetation there is at times damaged accordingly: density-dependent regulation is more likely to occur in these particular drylands.

Do the Sahelian floodplains act as a source for livestock numbers, and the wet-season grazing areas (that is, the dry 'bush') as a sink?

The ecological theory of sources and sinks implies that the reproduction rate of individuals or the production level of the animal population in the source area determines population size in the sink areas, and not the other way around. Illius and O'Connor (2000) calculated that their key resource area, if large enough, does indeed positively influence livestock numbers in the associated wet-season range. In the case of the Sahelian floodplains, however, there is also a reverse effect of the wet-season range on the livestock numbers in the associated floodplains.

Seasonally flooded grasslands in the Sahel are indeed areas with high production potential for livestock (Box 10.3), and also for wild herbivores. The Waza-Logone floodplain harbours the only national park with substantial floodplain habitat in the African Sahel. Waza National Park used to have a wild-herbivore density of more than 2000 kg km^{-2}, well above the curve of wildlife densities against rainfall plotted for West and Central African reserves with only limited floodplain areas (De Bie 1992). With the cessation of annual flooding in Waza National Park in 1979, due to the construction of a dam upstream, wild-herbivore densities dropped to about 1000 kg km^{-2}, well within the rainfall–wild-herbivore curve just mentioned. This drop in the floodplain herbivore density also caused a drop in herbivore densities in surrounding upland areas, where herbivores migrate to during the rainy season (Scholte et al. 1996). It is concluded that annual flooding was a crucial factor in the high productivity of the floodplain, with an impact on herbivore populations beyond the floodplain.

Similarly, the Lake Chad Basin, characterised by the large ratio of its floodplains to its wet-season ranges, has amongst the highest livestock densities in the African Sahel (Table 10.1B). In the World Atlas of Degradation (UNEP 1992), the Lake Chad Basin was also considered to be less degraded than similar areas in the Niger basin. Illius and O'Connor (1999, 2000) indeed predicted high animal populations for areas with a large key resource area ratio to wet-season ranges. We speculate that the relatively high hydrological variability of the Lake Chad Basin is compensated for by the relatively low percentage of agricultural land, compared to areas surrounding the other major floodplains of West Africa. This has allowed longer migration routes and enhanced use of the Lake Chad Basin by large grazers (see also Van Keulen and Breman 1990). All this suggests that the floodplains of the Lake Chad Basin have a positive effect on the density of large grazers in the surrounding drylands.

The point is, however, that the drylands and floodplains in the Lake Chad Basin do not exist next to, and more or less separate from, each other. They are both an integral component in the same annual cycle of the associated large grazers. Poor conditions in the drylands during the time of year that the floodplains are inaccessible will reduce numbers returning to the floodplains, but good conditions may increase those numbers. As far as large grazers are concerned there is therefore not a simple source–sink relationship between the floodplains and the drylands of the Lake Chad Basin

Does the presence of the Sahelian floodplains occasionally lead to an increased degradation of the wet-season grazing range?

Illius and O'Connor hypothesised that this would be the case, contrary to what Behnke et al. (1993) and Scoones (1995) suggested. Our conclusions are that the presence of the Sahelian floodplains does indeed occasionally lead to greater degradation of the wet-season grazing range than would be the case without them. See the discussion under the preceding question and under the first point of 'Spatial variability and density-dependence' above.

OTHER ASSUMPTIONS BY ILLIUS AND O'CONNOR (2000)

Does it matter whether the potential primary production in a key resource area, on a per-hectare basis, is assumed to be the same as in the associated wet-season grazing area?

No, it does not. Illius and O'Connor varied the ratio between areas of the key resource area and the associated wet-season grazing range. Doubling that ratio at constant potential primary production per hectare is equivalent to doubling potential primary production per hectare at a constant area ratio.

Does it matter whether plant growth in dry-season grazing areas, or key resource areas, is assumed to vary in synchrony with plant growth in wet-season grazing areas?

Actually, Illius and O'Connor did not look at intra-annual variability in forage availability. Working only with total annual forage production, they implicitly assume that this food is available throughout the year unless already eaten. They also make the explicit assumption that living and dead forage biomass are of the same quality, which clearly is not normally true (see, e.g., Beekman and Prins 1989; Prins and Beekman 1989; Prins 1996). It really matters whether the plant growth in dry-season and in wet-season grazing areas is assumed to vary synchronously. First, because in real life biomass quantity and quality vary enormously throughout the year (Breman and De Wit 1983; Prins 1988, 1996). Second, because *accessibility* of the dry-season and wet-season grazing areas often does not vary synchronously (Box 10.2). If accessibility varies asynchronously, then it can be very 'useful' if quality varies asynchronously as well. That way good-quality forage may be available as well as accessible at different times of the year in the two areas, so that the dry-season and wet-season grazing ranges can be as complementary a pair of forage sources as possible.

Does it matter whether dry-season and wet-season length, and access to the associated grazing ranges, are both set at six months of the year, instead of another ratio?

Within the constraints that Illius and O'Connor set themselves, it does not matter. Changing the ratio of area or potential primary production has the same effect on the modelling outcome as changing the ratio of dry- and wet-season length.

Are potential effects of key resource areas on surrounding wet-season grazing areas, including on species composition, perhaps related to forage accessibility as much as to forage availability?

As the modelling by Illius and O'Connor (2000) shows, the positive effects of their key resource areas on grazer numbers are greater when there is more restriction in the seasonal accessibility of the range areas. When there is no restriction in accessibility the effect on grazer numbers was as good as zero. It follows from this that potential effects of key resource areas on surrounding wet-season grazing areas, including on species composition, must indeed be related to forage accessibility. If the forage is there in the key resource area, but the grazers cannot get to it because of, for example, flooding, the associated dryland or wet-season grazing areas will be searched for the required food, whether they can provide it or not.

ADDITIONAL ASPECTS

Would the effects of a number of small key resource areas forming one grazing unit, such as a number of adjacent isolated wetlands, differ from the effects of one large key resource area?

There are two important sides to this: accessibility and forage production reliability. If, for whatever reason, it is not possible for grazers to move from one small key resource area to another, then the grazers are obviously better off with one large key resource area than with a number of small ones. If there is no problem with access, then the forage production reliability becomes important. If forage production in all the small key resource areas depends on the same hydrological events, then all the small areas will react to hydrological events as though they were one large area. But if the small areas have a certain degree of hydrological independence from each other, then it becomes a different story.

If grazers cannot move from one small key resource area to another, one large key resource area is better than several small ones

Rainfall events in the Sahel are often rather local storms. Over a distance of 5-7 km it is possible for total annual rainfall to vary from 600 to 850 mm in the same year (Wallace et al. 1994; see also Prins and Loth 1988 for East Africa). Small isolated wetlands, each with their own catchment quite close to each other, can therefore vary considerably in the degree to which they flood in a particular year.

This spatial variability reduces the chances of all wetlands flooding poorly, and producing forage poorly, in the same year. In this way a fragmented resource can be a more reliable source of food than a similarly sized resource consisting of just one hydrological unit.

Does it matter whether, in relation to key resource areas, the focus is so generally on forage instead of on water or some other factor?

What do grazers need? Food, water, and places for shelter, feeding and reproduction, all in the right (optimal) amount, in the right place and at the right time. Grazers also need a relative absence of factors that prevent the grazers from making use of these five factors. Food is necessary for grazers, but not sufficient. A key resource may therefore just as well be water, or a safe place, as forage. It is, of course, no coincidence that forage has received most attention, as it is, within the limits of access to water, the bottleneck in Sahelian grazing systems (Breman and De Wit 1983; Le Houerou 1989).

Production characteristics of herbivores with access to Sahelian floodplains

Large-scale migration is reputed to enhance livestock production (Breman and De Wit 1983; Le Houerou 1989; Niamir-Fuller 1999). Whereas sedentary livestock produced an estimated 0.4 kg protein $ha^{-1}year^{-1}$, transhumant migration into medium-rainfall area produced 0.6 kg protein $ha^{-1}year^{-1}$ and transhumant migration into the Inner Niger Delta floodplain was found to produce up to 3.2 kg protein $ha^{-1}year^{-1}$ (Breman and De Wit 1983). These production characteristics are in line with observed differences in livestock densities (Table 10.1).

As expected with the observed ideal free distribution (Box 10.3; Scholte 2005; Scholte et al. 2006), available data indicate that Fulani cattle from herds that have access to Sahelian floodplains have comparable production characteristics, expressed per head of livestock, as (semi-)sedentary Fulani herds that remain outside floodplains (Table 10.3). If any changes can be detected between herds under otherwise comparable conditions (as indicated by average annual rainfall), they tend to show even a somewhat lower production of individual cattle having access to the floodplain compared to those that do not have such access (Table 10.3). We hypothesise that this lower individual production is caused by the lower 'risk' of cattle in the floodplain. Imagine a 100-km^2 floodplain with 100 herds (of 100 cattle each) and surrounding dryland with 10 herds in an area of 100 km^2. A 'marginal herder', joining with his single herd of 100 cattle, poses for the floodplain herders a cost of 1% 'competition', whereas the dryland herders face a 'competition cost' of 10%. Only with 9 herds joining the floodplain and 1 the drylands, the cost will be comparable. We postulate that the number of conflicts indicating these costs is higher in the drylands than in the floodplain. Indeed, mostly qualitative information from the Logone floodplain suggests a very limited number of conflicts inside the floodplain compared to outside (Moritz et al. 2002). Differences in herd management, such as low labour costs of providing drinking water in the floodplain compared to outside the floodplain, might alternatively explain the somewhat lower production inside the floodplain.

When considering Sahelian floodplains as key resource areas, it is clearly not the production ('fitness') of the individual herds or individual animals that characterises these areas. In contrast, herds that receive supplementary feeding, show higher production characteristics per individual animal (Table 10.3). The analogy of key resource areas with supplementary feeding as indirectly suggested by Illius and O'Connor (1999) does not hold, at least not for Sahelian floodplains.

Table 10.3. *Comparison of Fulani cattle production with and without access to floodplains*[1]

	Cattle with access to the Inner Niger Delta floodplain				**Cattle without access to floodplains**			
	Herds lumped [2]			Years lumped	Mali[3]	Nigeria[4]	Nigeria[5]	Improved manage-ment [6]
Sample size	820	910	879	2550	734	?	1367	?
Year	1979	1980	1981	1979-81	1979-81?	?	?	?
Average annual rainfall (Table 10.2)	± 500mm				± 500 mm	±850 mm	±1050 mm	±500mm
Cow viability (%)	0.95	0.92	0.94	0.92	0.97	0.97	0.96	0.97
Calving rate (%)	0.55	0.58	0.55	0.54	0.57	0.45	0.46	0.77
Calf viability (%)	0.79	0.50	0.62	0.64	0.75	0.86	0.88	0.69
Calf weight at 1 year (kg)	85	80.3	73.0	79.6	81	91.1	80	125
Milk off-take (kg)	266	205	185	218.6	193	286.4	234	522
Prod. index (cow/yr)	49.9	33.6	34.0	37.2	45.7	47.5	42.5	108.8
Adult cow weight (kg)	215				242	268	245	302
Prod. index [7] (year/100 kg cow LW)	23.2	15.6	15.8	17.3	18.9	17.7	17.3	36

[1] Adapted from Wagenaar et al. (1986)
[2] Herd R and S (with 210 cattle each), following the same grazing orbit, and V (with 400 cattle) had a prod index (year/100 kg cow LW) of 20.7, 15.6 and 15.8, respectively (averaged over 1979-1981)
[3] Agropastoral system, Niono, Mali (Wilson 1983)
[4] Settled Fulani, Kaduna Plains, Nigeria
[5] Settled Fulani, Jos plateau, Nigeria
[6] Sudanese Fulani cattle under improved management, Niono, Mali
[7] [cow viability × calving rate × calving survival × calf weight at 1 year (kg)] + [cow viability × calving rate × milk offtake (kg) divided by 9)].

SYNTHESIS

What makes an area with resources in it a so-called 'Key Resource Area'? Illius and O'Connor (1999, 2000) have tried to give a quantitative definition, but according to that definition the floodplains of Waza-Logone are not key resource areas for the pastoralists and their livestock that use them. These floodplains diverge from that definition in that they are not the only resources that regulate grazer numbers in the associated grazing system. If, however, these floodplains were no longer available to those pastoralists, their grazing systems would change dramatically, and cattle numbers would probably be reduced substantially. In the case of the floodplains of Waza-Logone, the alternative would be for the pastoralists to migrate further south for the dry season. The costs of migration southward to areas with more reliable rainfall, and forage, including the time and energy needed to cover the relatively long distance, are high. Associated with these direct costs, there is an increased risk of exposure of the livestock to diseases that are more frequent in higher-rainfall zones, and the need to pass through agricultural areas with little available grazing, but also an increased risk of conflicts with farmers (Kari and Scholte 2001).

Important for KRAs is that the resource is accessible when a comparable resource is not accessible in sufficient quantity and/or quality elsewhere

For the floodplains of Waza-Logone and other floodplains in the Sahel, it is therefore not the previously assumed low inter-annual hydrological variability that explains their importance to the pastoralists that use them. Rather, it seems to be the availability of 'good'-quality forages in 'fair' quantity especially in the beginning of the dry season, combined with 'low'-quality forages in 'ample' quantity throughout the dry season, coupled to a relatively low risk of complications of resource accessibility and livestock diseases, which explain the relatively high livestock densities in the floodplains. Put differently, what the pastoralists involved most likely seek is not so much low variability as high 'assured' production and reduced risk. It is therefore not so important whether a particular area produces more and/or better forage, or another resource, than do other parts of the grazing system. What *is* important is that in such an area the resource is *accessible* to the grazers at a time of year, or in a year, when a comparable resource is not accessible in sufficient quantity and/or quality elsewhere in the grazing system.

Our alternative definition of a key resource within a grazing system is therefore "a spatially defined resource that allows a grazing system to maintain one or more populations of herbivores in disproportionately higher numbers than could be maintained without that resource"; a key resource area is the area where this key resource is found. Based on this definition, we postulate some hypotheses for future research (Box 10.4). Our definition, like the definition of Illius and O'Connor, implies that:

Key resource allows a grazing system to maintain herbivores in disproportionately higher numbers than could be maintained without that resource

a. Other parts of the grazing range are more heavily utilised by animal populations sustained by key resource areas, than would the case in the absence of the key resource areas.
b. The key resource area does not necessarily act as such every year: it may be the key to understanding population dynamics of a larger area only during extreme years.
However, this definition expands on the definition and its application by Illius and O'Connor (1999, 2000), and acknowledges that:
c. Herbivore numbers are not necessarily regulated in a density-dependent manner by the limited resource available in the key resource areas. Herbivore numbers may, as in the case of Sahelian floodplains, be merely controlled, without feedback with the grazing resources.
d. Temporal variability in the availability of the resource concerned need not be less than temporal variability in the remainder of the grazing system, and can even be greater. However, if such variability is greater than that of the remainder of the system, it is most likely important that it is also asynchronous with the variability of the remainder of the system.
e. The key resource need not be a dry-season resource nor necessarily be food, it can also be water, or a lack of predators or disturbance or pathogens, or another factor essential for grazer existence and reproduction.
f.. Although total production is increased through the presence of a key resource area, this does not necessarily hold for the individual herbivore and depends on the distribution model. A key resource should not be considered as a kind of supplementary feeding.

Box 10.4. *Testable hypotheses for future research*

Hypothesis 1. Sahelian floodplains are characterised by a high livestock density and resulting high animal production per unit area. We showed that it is not the previously assumed low inter-annual hydrological variability that explains their importance for pastoralists. We postulate that the availability of 'good'-quality forages in 'fair' quantities especially in the beginning of the dry season, combined with 'low'-quality forages in 'ample' quantity throughout the dry season, coupled to a relatively low risk of complications of resource accessibility and diseases, explains the high livestock density. What pastoralists seek is not so much low variability as high 'assured' production and reduced risk, which spatial and temporal variability in food availability and accessibility can help achieve.
Hypothesis 2. In a system with Ideal Free Distribution, the presence of high-quality forage ('supplementary feeding') may lead to increased herbivore densities and subsequent increased total animal production, but not to increased individual herbivore production.
Hypothesis 3. A key resource within a grazing system is a spatially defined resource that allows a grazing system to maintain one or more populations of herbivores in disproportionately high numbers compared to what could be maintained without that resource. A key resource area is the area where this key resource is found.
Hypothesis 4. A grazing resource fragmented over several hydrological units is a more reliable grazing area than a similarly sized resource located in just one hydrological unit.