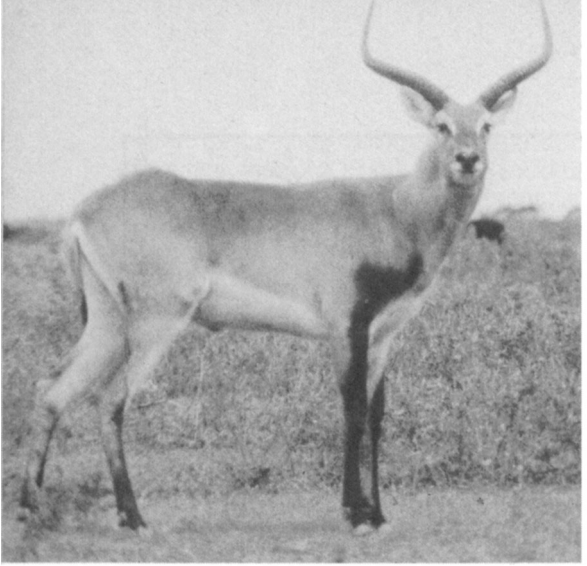

Will the Kafue Lechwe Survive the Kafue Dams?

Richard Schuster

In the early 1970s the huge lechwe herds gave the Kafue Flats in Zambia one of the highest carrying capacities in the world – an estimated 11,000kg per sq km. But these highly specialised antelopes depend on the annual floods of the Kafue river, to which particularly they have adapted their breeding behaviour and the leks in which they mate. Since the completion of two huge dams on the Kafue these floods are now controlled in the interests of making electricity, and not of the lechwe. The author, who studied the lechwe's social organisation and behaviour in the Lochinvar National Park, first describes the lechwe's remarkable lek system, how they are adapted to the floods to the point of being able to graze in water up to their shoulders, and the remarkable way in which they maximise the resources of the Flats. In the second part (page 481) he shows how the new flood control can disrupt their breeding behaviour and social organisation, which might lead to the extinction of the Kafue lechwe.

The lechwe antelope *Kobus leche* of the Central African floodplains has been a threatened species for many years. Due mainly to hunting, all three subspecies have declined in both population and distribution: the red lechwe *K. leche leche* of the upper Zambezi and Kafue Rivers and the Okavango swamp; the black lechwe *K.l. smithemani* of the Bangweulu floodplain of Zambia; and the Kafue lechwe *K.l. kafuensis* of the Kafue Flats floodplain in southern Zambia.[1 3 4 29] Only remnants now survive of the huge grazing aggregations that awed observers earlier in this century. In the early 1960s, one population, numbering perhaps 25,000-35,000, increased rapidly following a complete ban on hunting and the creation of two small national parks.[2 4] But recent hydroelectric development of the Kafue River, by interfering with the natural flood cycle on the floodplain, poses a new and irreversible threat.[32 37 39 40]

In August 1974, when the annual floods were still more or less normal, the author began a study of the Kafue lechwe's social organisation and social behaviour in Lochinvar National Park, on the southern bank of the Kafue, to see whether this system could be sustained after flooding changes. By March 1977 the changes in the flooding cycle were sufficient to interfere with

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COUNTLESS THOUSANDS *Mark Boulton*

breeding behaviour. It is also certain that the lechwe will decline as a result of reduced floodplain grazing.[37] If lechwe are to survive, recruitment must at least compensate for deaths by natural causes and poaching. So it is vital to understand the lechwe's mating system and the conditions that support it in order to anticipate the full impact of the new conditions, and to design possible cropping or transplanting schemes. This paper, updating an earlier report,[39] outlines the relationship of the natural floodplain ecology to the lechwe's mating system, and discusses why the changed flooding conditions pose a serious threat.

A Floodplain Antelope

The lechwe is specialised in many interconnected ways for a floodplain existence. Rarely grazing far from water, lechwe can often be found grazing in water up to shoulder height, and readily take to water when threatened. Their movement in water is facilitated by their elongated hooves and high hindquarters – about 10 per cent higher than the forequarters.

In other respects, they are typical of many gregarious, grassland antelopes. Males are larger than females, averaging over 100kg compared with about 70kg, and only males carry horns, which are double curved. The Kafue race is distinguished by an impressive horn size (average 72cm, N156), and by the extension of their black leg stripes into wide shoulder patches that stand out against their reddish brown pelage and white underside.

By invading the virtually uncontested niche of the floodplain, lechwe almost completely avoid many effects of the long, dry season. Zambia has at least six consecutive dry months, but the floodplains provide fresh grazing almost the whole year round. The flooding creates fresh grazing that gradually becomes available as the water level falls in the second half of the dry season.

In countless thousands the lechwe move back and forth with the changing

GRAZING IN WATER

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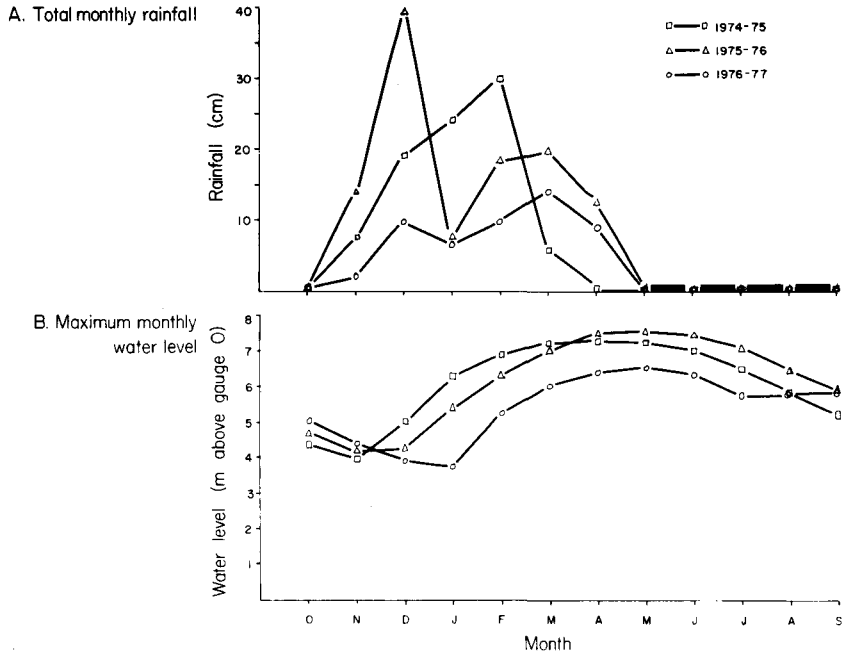

flood levels, bringing the carrying capacity of the floodplains up to an estimated 11,000kg/sq km, among the highest in the world. During the early 1970s, the 200 sq km floodplain area of Lochinvar National Park supported some 40,000 lechwe, along with smaller herds of zebra, wildebeest and eland.

An important feature of the natural flooding cycle was its delayed timing in relation to rainfall[47]. The peak floods occurred three to four months after the peak rains, and the flooding occurred for the same reason that a sink overflows when the tap is full on but the drain is blocked. The narrow Kafue Gorge at the outlet of the plain was the blocked drain and the excess water came from the heavy seasonal rain between November and March that drained into the Kafue River from much of Central Zambia. Most water came from north of the floodplain, where rainfall is up to twice as high and most of the tributaries flow into the Kafue. On the Flats, with their low gradient – a fall of only about 15m over a channel length of 450km – the water moved very slowly. By the time the maximum flood reached Lochinvar between April and June, the rain had long since ceased.

For the lechwe, the gap between rainfall and flooding peaks imposed annual cycles in body condition and reproductive activities and a seasonal rut. These are schematised above. The key to the regulation was the flooding cycle which governed the availability of the grazing. Studies of rumen contents showed that floodplain species were clearly preferred; others were grazed more during the high flood, when the herds were forced off the deep floodplain on to the shallow Nampongwe floodplain and 'termitaria'.[20] When the floods remained high for long periods, overgrazing became a problem.[34] Also once the rains had finished, much of the exposed forage had ripened and dried off, resulting in the reduced body weight and kidney fat that has been described as 'nutritional stress'.[4 34 37]

The emphasis on 'stress' is somewhat misleading. The high flood affected adult males and females differently. Males suffered a seasonal decline, but kidney fat had begun to decline during the rut which takes place in the rains,

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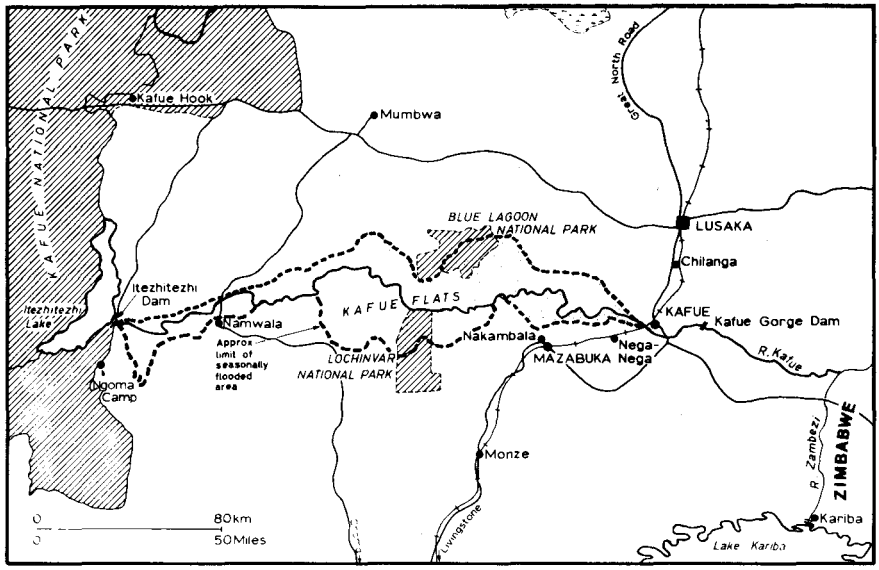

Dotted line shows extent of flooded area before the dams were built.

well before the high flood, and is typical of seasonally rutting ungulates. Males store up fat reserves which are expended on the increased aggression of courtship and rutting. Real stress has been reported when the high flood was much prolonged.[34] During the present study, males examined during the period of high flood were mostly in good physical condition. The one consistent effect correlated with the high flood was a drop in testis weight, indicating that reproductive condition had reached its lowest annual level.[34 37]

When the floods began to go down, but long before the rains started, the herds re-entered the floodplain. The males began to restore their body and reproductive condition until they achieved peak condition about the time that water levels were at their lowest. The annual rut then began and continued for about three months during the rains while the flood levels rose, so that throughout the rut herds were slowly moving towards higher ground.

For females, now mostly pregnant, the rising floodwaters coincided with the time of *highest* kidney fat percentage, which only gradually declined after the rains ceased. The different body cycles in males and females suggest that nutritional stress was perhaps partly caused by their different grazing patterns. Observations of herd locations showed that male herds generally moved earlier and also over greater distances in response to the changing flood levels.[34] During high flood, males aged three years and over were mostly found far from water, in areas of dry grass and even in woodland fringes. Females and young remained in the one area of Lochinvar that still contained quantities of fresh, accessible grazing, the so-called 'water meadow grassland' where there was a variety of shorter stemmed rhizomatous species. These observations confirm Geist's prediction (1974) that such differences can exist when it is adaptive for males to give up prime grazing to pregnant or lactating females.[16] When the floods began to go down males again moved sooner and travelled further on to the floodplain where they regained condition for the coming rut.

The timing of the rut also guaranteed that the majority of lambs were born between July and September when the falling water exposed fresh grazing to the lactating mothers, and the tall, waterlogged grassland provided cover

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where young lambs would lie motionless except during lactation.

The conditions for rutting, however, did not restrict all reproduction to three months. As in past years some mating was observed throughout the year, and a few newborn lambs could be seen at all times. This made it possible to compare mating systems and reproductive behaviour under different ecological conditions, which could provide useful clues to the lechwe's capability of reproducing in the future.

The Lek

During all the rutting seasons observed, the Kafue lechwe used a *lek* mating system.[38 39 42] Fully developed lekking in antelope occurs regularly only in the closely related Uganda kob *Kobus kob thomasi;*[5 6 25] topi *Damaliscus korrigum* use leks under some conditions.[30] A scattering of birds, insects, and mammals also use a lek mating system.[13 48]

In the classic lek adult males, sometimes more than 200 of them, gathered on a communal display ground used for mating, where individuals occupied a cluster of tiny territories. Those that did not acquire lek territories, the bachelors, collected elsewhere. Moreover, having a lek position was not enough to ensure mating success. Arbitrarily, a more or less central territory, or at most two or three, became 'mating centres' where the possessing male(s) enjoyed high reproductive success. The oestrous females, upon entering the lek, almost invariably chose a mating centre for copulation. Thus males engaged in a double competition, first for a lek territory and then for a central location. Oestrous females, by entering the mating centres, were assured of choosing a fit male for mating.

It is also typical of lek systems that the clusters were easy to locate. The close gathering of males, each visibly and vocally advertising himself, advertised the gathering and attracted females. The leks were on open or slightly elevated ground easy to see, and in the same places from year to year, a form of 'tradition' documented in kob for 15 years.[7]

In many respects, leks are but one variation among the vast majority of mammalian mating systems in which some of the adult males mate with a disproportionate share of the females. The evolution of such polygynous systems is believed to occur when males, needed less for parental duties, are freed to maximise their genetic fitness by mating more often.[48] This results in competition for females and sexual selection, the evolution of characters such as greater size, weapons, and competitive behaviour.

Why a lek form of polygyny existed on the Kafue floodplain requires explanation. The mating system of the congeneric waterbuck *K. defassa,*[44] which is typical of the polygynous mating systems of many grassland antelopes, shares many features with a lek: a territory is needed for mating; only males compete for territories; territories are clustered; individual territorial males can be more successful than others, depending upon how many females choose to enter.[21 26 31] Within the boundaries, food and perhaps water resources are being defended mainly against other adult males, so that territories are larger. Females, attracted by the resources, enter and are mated by the defending male. Success is determined by the location and quality of his territory – 'better' territories attract more females. Although resources are being defended, the territorial cluster is really functioning as a mating system, described as 'resource defence polygyny'.[12]

On a lek, females choose a male by the location of his territory, which is *arbitrary*, a fixed place somewhere in the centre of the cluster. Resources are not being defended, and the female's choice of mate is based only on location. The territories may as well be small because, from a resource point of view, they offer nothing. Determining the 'best' male becomes a matter of going to the mating centre, distinguished by its trampled turf, odours, and cluster of female visitors, and occupied by a male able to defend it and to copulate frequently.

The leks on the Kafue floodplain took place where there was rich grazing and so little value in defending a patch of grass; it was not a 'defendable resource'. A system of territorial competition thus became a competition directly for mates.[12] The lek also drew females from wherever they were grazing, which might be some distance. Group display, open exposure, and traditional placements would all have compensated for the absence of resources as a means of attracting females to the mating area.

After Flood Regulation – What?

The survival of the lechwe on the Kafue floodplain hinges on three factors:

1. What conditions will exist on the floodplain after regulation?
2. Will the conditions support the lechwe's mating system?
3. Is the lek system critical for maintaining reproduction at a level at least sufficient to stabilise future population?

The answers cannot be known for certain in advance, and prolonged monitoring is needed as conditions change. Nevertheless, there are already serious grounds for concern.

The danger posed by ecological change has been added to other problems with a long history that is full of paradoxes.[2 29] Cattle ranching in Africa is often cited as a main reason why wildlife has disappeared, yet lechwe survived on the Kafue Flats only because the owners of two large ranches, Lochinvar and Blue Lagoon, protected the remaining herds from poachers and allowed them to share the rich floodplain with their cattle. At the same time predators were removed and other ungulates severely reduced. In 1933, the ranches became Game Management Areas and after that were bought by the Zambian Government. Both were made national parks, Lochinvar in 1972, Blue Lagoon in 1973. The lechwe population increased to over 90,000,[4] but under park status the population fell to 80,000 in 1975[36] and 70,000 by 1977, just before flood regulation began in earnest. The most recent estimate is about 50,000. Ironically, much of the blame has been placed on *over*population. The confinement of 90,000 animals, it was said, caused serious overgrazing and disease, especially tuberculosis.[4 37]

But the lechwe is normally a most gregarious antelope, and a prolific breeder.[17] Historical descriptions of vast aggregations are consistent with observations today of grazing lechwe in groups of hundreds or thousands, especially in the black lechwe of the Bangweulu floodplain, where the 1972 population of about 16,000 was highly concentrated despite a huge floodplain area. Nutritional stress cannot be a critical issue if it affects males more than females, and an extremely polygynous mating system can tolerate higher male mortality without affecting recruitment. Nor does tuberculosis seem to be a killer. Infected animals, even with extensive lung lesions, were regularly seen to be robust.[35]

Poaching for Meat

As in earlier times, poaching seems to have been the main cause of high mortality. Gunshot or spear wounds were the cause of *all* deaths in more than 100 carcasses in which the cause could be ascertained.[36] The persistence of large scale poaching was hardly news; excessive hunting has always been the problem.[43] Lechwe meat is a traditional favourite with Zambians, and decades ago black lechwe were slaughtered by the thousands for sale in the Copperbelt.[4] Until 1957 Kafue lechwe were killed by the hundreds in legal organised hunts known as 'chilas'.[29]

Solutions are not obvious. Poaching clearly paid, and the outnumbered guards and wardens were easily persuaded or intimidated by local villagers whom they got to know. Fines were small, and guns and vehicles were returned intact. Frequently the meat, the only evidence that secured a conviction, somehow disappeared.

During the 1960s, Kafue lechwe increased rapidly despite poaching, but if flooding changes lead to large reductions in population and recruitment, the same amount of poaching could deliver the *coup de grâce*. And such changes seem possible.

Effect on the Habitat

Deterioration of the habitat is one inevitable consequence of the hydroelectric scheme. Zambia's need for electric power required a more secure site than the Kariba Dam on the Zambia-Zimbabwe border; the narrow Kafue Gorge was a logical choice and the dam was completed in 1972. But, because the flat floodplain behind was not suitable for a storage reservoir, a second dam was built at Itezhitezhi, the inlet to the floodplain, to ensure an even flow of water to the power dam by holding back flood water outside the floodplain, then releasing it gradually over the year. This means that a smaller area will be annually flooded and a larger area permanently flooded, the latter because of a combination of back-up from the lower dam and a level of regulated flow from the upper dam that exceeds the river's capacity.[28] Both effects were seen in 1976/77 as the regulating dam neared completion. The water level was higher in the 1976 late dry season and fell more slowly, continuing well into January. In August and September 1977, the water level, which usually fell before the crucial rut, remained constant, and correspondents report that high levels are still being maintained.

Taken together, these changes must lead to a further big decline in the lechwe population. In a habitat of such low gradients, a small increase in water level means large areas permanently inundated, some of which will be inaccessible to the lechwe. Moreover the grass species will change; patches of papyrus now occur in areas once covered with the lechwe's favoured floodplain grasses.

The designers, aware of the flood's importance for the ecology, planned for some inundation every year, so that, even in years of low rainfall, some would be released in March.[47] But this would produce only a very small flood which, given the evaporation losses and flow patterns across the Flats, will only minimally influence the middle and eastern parts of the plain. Even in years of good rainfall, flood levels will be lower and last longer.

If electric power is the priority, the total area flooded annually will be reduced, and lechwe will be forced to graze more at each location. In former

years, when high flood levels were prolonged, malnutrition and mortality in the lechwe increased.[34] In areas that receive little or no flooding, coarser tussock grasses are expected to replace favoured and more nutritious floodplain species, as was observed under natural conditions in 1963/64 when abnormally high floods one year were followed by abnormally low floods the next.[45]

To appreciate the danger posed by flood regulation, it is only necessary to recall that the area of grazing uncovered by the falling water was the crucial resource for the lechwe in the late dry season. This was the main supply of fresh forage before the rut, and probably the ultimate determinant of the floodplain's ability to carry a high population despite several dry months.

Can the Lek Mating System Continue?

The second factor is whether the deterioration of the floodplain will lead to the disruption or disappearance of the lek mating system. Resources could be indefensible because they are *abundant*, or *unpredictable* in space and/or time. If *Kobus* leks are typical, abundance seems more critical. The Kafue floodplain was both a fluctuating habitat and abundant in grazing both before and during the rut. Uganda kob are lek-forming where abundance is combined with stable conditions that eliminate all herd movements and all seasonality; kob lek throughout the year on a network of more or less fixed locations.[6 7]

Rich resources go with a large, dense population, which may also create social conditions that are critical for lekking. Kob do not lek where population densities are low, and neither do lechwe. Red lechwe, surviving in small, scattered populations over a wide area, have not been seen to lek. Kafue lechwe show the same variation seasonally. When they mate outside the main rut, leks do not form. The few sexually active males take up stationary positions, perhaps territories, although there is almost no active defence. Such males are found either in isolation or within loosely organised groups of sexually inactive males.[39]

Moreover, the particular and in some ways unique form of the lechwe's lek system was determined by herd movements caused by the flooding cycle. Lekking occurred when water levels were rising during the rains. In contrast to the static leks of the kob, lechwe used a succession of fixed lek locations, each for a brief period, at progressively higher elevations as the herds slowly moved from the deep floodplain, where the first location was found, towards the termitaria, where the last were found. In the study area, there was a succession of six locations. Changes in the flood level governed the timing of lek use. Table 1 lists the approximate dates of lek operation between 1974 and 1977 (approximate because observation was not continuous). In each year, there was a progressively later date for both organising and abandoning each location. This correlates with the progressively later fall and rise in flood levels over the same years. Rainfall did not correlate with lek use. In 1975/76, for example, the rain was usually early and heavy but it did not accelerate the lek season. In 1977, delayed flooding led to a static situation in which one lek was sustained.

The altered flooding cycle during the 1976/77 rutting season may have provided a glimpse into the future. Following the delayed drop in the flood level in the dry months of July through November 1976, the lek season was significantly disrupted. Of the six lek sites used in previous years, only three

TABLE 1 Lek Utilisation – 1974-77

LEK	1974/5		1975/6		1976/7	
	Organized	Empty	Organized	Empty	Organized	Empty
1	1 Nov.	14 Dec.	21 Nov.	4 Jan.	2 Dec.	31 Jan.
2	3 Nov.	14 Dec.	5 Dec.	4 Jan.	3 Dec.	14 Jan.
3	5 Dec.	28 Dec.	4 Jan.	28 Jan.*	14 Jan.	27 Feb.*
4	14 Dec.	28 Dec.*	25 Jan.	26 Feb.		
5	28 Dec.	–	25 Jan.	26 Feb.	not organized	
6	28 Dec.	–	28 Feb.	1 Apr.**	not organized	
A	not existing		not existing		31 Dec.	27 Feb.*

* still operating; not observed thereafter ** males still present; but lek distintegrated

TABLE 2 Comparison of Lek Population and Aggression in 1975/6 and 1976/7

1975/6

Lek	No. males	Hours observed	Total aggression	Aggression/ hour
1	85-100	6.0	98	16.3
2	100	2.9	89	30.7
3	180	4.7	509	108.3
A	not existing			
	Total 1245	13.6	19.5	

1976/7

Lek	No. males	Hours observed	Total aggression	Aggression hour
1	20-30	13.2	51	3.9
2	25-140	17.5	255	14.6
3	60-25	7.9	74	9.4
A	75-200	25.3	865	34.2
	696	51.1		63.9

TABLE 3 Comparisons of Reproductive Behaviours in Kafue Lechwe on and off Leks

Social environment of courting male	Lek	Isolated	Other males
Hours courtship behaviour observed	62.5	14.2	18.1
Courtships initiated: Total	216	57	73
Frequency	3.5/hr	4.0/hr	4.0/hr
Copulations: Total	29	2	17
Frequency	0.46/hr	0.14/hr	0.94/hr
Proportion of initiated courtships	.13	.04	.23
Average uninterrupted courtship time to copulation	7.8 min	13.5 min	9.9 min
All pre-copulatory behaviours: Total	2,438	530	1,099
Frequency	39.0/hr	37.3/hr	60.7/hr
Pre-copulatory mounting: Total	1,673	219	434
Frequency	26.8/hr	15.4/hr	24.0/hr
Proportion of all pre-copulatory behaviours	.69	.41	.39

were seen (Table 1), and two, 1 and 3, were much less active (Table 2). Aggression was reduced, central males were not pressured, females were not tightly clustered, and a few subadult males were able to hold places. Most revealing, total participation was drastically reduced (Table 2), probably because high flooding during the late dry season resulted in fewer males reaching prime condition for rutting. The picture is complicated by the emergence of lek A not seen before. Possibly lek A alone could have compensated for the desultory conditions on the others, though it is unlikely.

In a tentative way, these changes warn us that the lechwe's reproductive social organisation is sensitive to the flooding conditions and the availability of floodplain grazing. At the very least, the leks will be disrupted in the future. The complete disappearance of the lek system is a possibility.

The overall reduction in population density might be one factor. A more direct cause could be the scarcity of good grazing in the late dry season where formerly great quantities were exposed by the falling floodwaters. The few animals reaching prime condition might benefit more by contesting scarce floodplain resources, leading to a dispersed resource-defence territorial system closer to that of the waterbuck.

Is the Lek System Critical?

The most problematic factor is whether Kafue lechwe can maintain sufficient recruitment rates if the lek system ceases to exist. Clearly, lechwe and kob both reproduce off leks under natural conditions. Kafue lechwe present the interesting example of a population that uses at least two different mating systems in different seasons. Other species use mating systems that are territorial at lower population densities and hierarchical at higher densities when greater numbers must coexist in the same location.[12 48] This parallels the transition from resource-based mating territories to a lek. Though still essentially a territorial mating system in which females are selecting males by location, the lek incorporates features of a hierarchy. The denser aggregation of males is dominated, both reproductively and aggressively, by the male(s) on the mating centre.

To show that lechwe can reproduce both on and off leks, however, is not to say that they do so with equal success. Small peripheral populations of all three lechwe subspecies have shown a tendency to decline and eventually disappear.[9 18 37] Large, core populations, on the other hand, are capable of maintaining themselves or increasing, with or without poaching pressure. Since large populations are implicated in a lek system, it is conceivable that lechwe can only maintain a high reproductive rate with a 'critical mass' of animals that leads to lekking. In kob, the lek system was responsible for nearly 100 per cent female pregnancy every year.

A lek could be vital for lechwe because their social behaviour patterns become better adapted to a crowded, highly competitive system of small territories than to a dispersed territorial system. There is evidence that the social behaviour patterns of both species are specially fitted to lekking.

One example is injury-free aggression. Lechwe fights invariably harmed neither contestant. In contrast, although waterbuck rarely fought, injuries and scars were commonplace.[44] The difference is consistent with the predictions of ethologists that more intense competition selects for increasingly ritualised forms of interaction, substituting threats for fighting.[27] Although it is arguable

whether ritual is the correct description for the lechwe's chasing and fighting,[41] the selection for injury-free aggression is undeniable.

Reproduction behaviour ought also to be specialised for lekking. In Uganda kob, the chain of courtship rituals may have become shortened in order to achieve rapid copulation on small but crowded mating territories.[8] Also, females were drawn only to leks. Although males were found on both leks and larger 'single' territories, only lek males had significant reproductive success.[25] Most of the lechwe young were conceived during the lekking season.[34 37] Copulation was not observed either in isolated males, presumably territorial, who were usually without females, or in males who led 'nursery herds' of females and young.

Outside the main rutting season, when there were no leks, males were sometimes associated with female clusters and engaged in typical antelope courtship. When the males were *isolated* from other adult males, successful copulations were rare. Comparing the first two columns of Table 3 shows that isolated males and lek males initiated courtships at similar rates and had similar overall frequencies of precopulatory behaviour. Yet lek males mounted more, required less time to copulate, and overall were roughly three times more successful in achieving copulations, measured both in frequency and proportion of initiated courtships.

It appears, therefore, that the social environment of the lek was a vital factor in the success of sexually active males. Unlike isolated males, central lek males were surrounded by other non-courting males who were presumably in reproductive condition. Central males also frequently defended their status, averaging 9.0 interactions per hour, many of which interrupted courtship. Yet their reproductive performance was superior. On a lek, defence and dominance could be significant factors in priming central males for reproduction.

How Neighbours Helped

There is also evidence that the mere presence of males nearby was sufficient to improve performance. Outside the lek season, courting males sometimes had male neighbours. In one situation seen only during the high flood period on the watermeadow grassland, females were grazing, and a few courting males occupied large, dry termite mounds which were widely separated, the distances being more typical of single-territory systems. There were very few aggressive interactions and displacements. Another time, courting males were surrounded by other males showing no aggression. In both situations, the reproductive performance of the courting males was facilitated by having neighbours (Table 3, column 3). In some respects – including copulations – these males were superior to lek males although there was no interference from aggression off leks.

The explanation for these behaviour differences is obscure. Perhaps adult males have higher outputs of sex hormones during the main lekking season, but hormonal differences alone could not account for the improvement of reproductive performance in non-lekking males that have male neighbours unless this factor is itself responsible for inducing the release of additional hormones. Equally, females could be influenced by the presence of crowded males. Whatever the proximal mechanism involved, it appears that the presence of other males has an overall *motivating* effect upon the sexual

performance of courting males, resulting in more efficient courtship and more frequent copulation.

Conclusions

From these data, it is possible to suggest that a lek mating system is a crucial factor in lechwe reproduction. This will need to be carefully tested in the coming years as the floodplain is progressively altered. Leks attract females and in some way motivate males. Although reproduction is possible on dispersed, resource-based territories, there should be concern that lechwe reproductive behaviour has become so specialised for a lek system that overall recruitment will suffer if the ecological conditions for lekking are eliminated. The situation could be further aggravated if the overall population density declines to a level where lechwe males are courting in isolation.

The conclusions are consistent with new discoveries about relationships between ecology and ungulate social systems. The lechwe provide perfect support for a theory explaining the evolution of temperate-zone ungulates entering rich, empty areas opened up by the retreating glaciers of the Ice Age.[16] This 'dispersal theory' also predicts remarkably well how the lechwe adapted to the rich floodplain: abundant resources lead to a large and healthy population. A seasonal rut provides intense competition among males, selects for large and vigorous males with exaggerated weapons, and also for specialised social systems in which violence is minimised in favour of injury-free forms of aggression.

A corollary of the dispersal theory is especially relevant to the lechwe's future prospects on a modified floodplain. Colonisers typically evolve to be specialist species that possess a variety of interrelated structural, behavioural and organisational adaptations for their richly endowed but geographically limited environments. The degree of lechwe specialisation is apparent from comparing the distributions of waterbuck – continuous from south of the Sahara to southern Africa – and lechwe, restricted to a few isolated floodplains. (Another lechwe, *Kobus megaceros*, is found only in the swamps of southern Sudan.) Ecological specialists are also found in rich, tropical environments, particularly rain forests. Because of high productivity and constant, reliable resources, rain forests typically contain a greater diversity of species, each finely adapted to a restricted niche.[22] The floodplain, by storing water that gradually rises and falls, duplicates many of the constant and richly productive conditions of the rain forest.

Ominously, the lechwe appear to share a characteristic associated with species of both rain forest and ice age dispersal – *inflexibility*. Finely adapted to a limited set of conditions, they become unsuited to disperse into new habitats or adapt to change in existing habitats. In fact specialists are the most vulnerable to extinction in the event of ecological change. Geist points to the fossil record of North American ungulates, littered with large-sized, large-horned species that presumably could not adapt to climatic change and became extinct.[15]

The message is obvious. The safest future for the Kafue lechwe is to preserve enough of the original floodplain ecology by means of artificial regulation to ensure a large population and a lek system. But the prospects that such a compromise will be reached are not bright. The needs of wildlife and agriculture depend upon extensive annual flooding. The demand for

maximum electrical power requires that the variations in water level be reduced as much as possible. All evidence at present suggests that regulation is changing the ecology of the floodplains in ways that will not suit the lechwe. With poaching still uncontrolled and a large population decrease almost inevitable, Kafue lechwe once again should be regarded as on the road to possible extinction.

Abstract: Hydroelectric development of the Kafue River in Zambia is changing the natural flooding cycle of the Kafue flats, and with it the principal mating system of the Kafue lechwe. Under normal conditions, the lechwe used a sequence of temporary lekking sites according to the changing flood levels. The lek organisation developed as the flood levels fell in the late dry season; at other times, some mating activity occurred without a lek system. The lek appears to have derived from a resource-based territorial mating system that became adapted to the resource-rich Kafue River floodplain, where fresh grazing was abundant during most of the year. Reproductive and aggressive behaviour were specialised for lekking. Females were attracted to lek sites, the sexual behaviour of males on central lek territories was facilitated, and threatening and fighting were frequent but injury-free.

The lechwe should be regarded as highly specialised for a floodplain existence. The new flooding conditions are almost certain to cause a marked decrease in population. The lek mating system will either be severely disrupted, as occurred in 1976/77, or entirely eliminated. Future recruitment could be too low to overcome mortality from the deteriorated floodplain and intensive poaching.

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