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CHAPTER 3
REDUNCINE ANTELOPE OF THE ZAMBEZI BASIN

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3.1 INTRODUCTION

The Reduncini (also known as reduncine antelopes) is a tribe of large to medium sized antelopes found only within Africa. It comprises a diversity of waterbuck, reedbuck, puku, lechwe and kob. According to the established taxonomy (Ansell 1971), at least ten species encompassing numerous subspecies have been described to science. Two genera are recognized, namely *Redunca* and *Kobus*. With one exception, all extant reduncine antelopes share a predilection for wetlands in the African tropics: these wetlands are all located within the savanna biomes of south-central and northern Africa. Reduncines are reliant on surface water, and so do not occur far from perennial water bodies. These antelopes have evolved distinct adaptations to an aquatic life, exemplified by the elongated hooves of lechwe. They are entirely grazers and are gregarious, living in small family units (waterbuck and reedbuck) or large herds (lechwe and kob).

An especially high diversity of reduncine antelopes is centred in and around the Zambezi Basin. Several endemic populations of lechwe are restricted to within certain Zambezian wetlands: well known populations occur on the Kafue Flats, Bangweulu Basin and Okavango Delta. At least 16 distinctive populations affiliated to complexes of four species of lechwe occur within the modern limits of the region. The origins of this high diversity deserve detailed study but this has yet to be carried out. Until recently, very large herds of lechwe and equally large collective populations of waterbuck, puku and reedbuck occurred within suitable habitats in the Zambezi Basin. Numbers and distributions of all these populations have shrunk radically in recent decades. The role of these antelopes in the ecology of the wetlands, where a high biomass of herbivores concentrated, was likely to have been profound.

The huge herds of charismatic lechwe and kobs on open sunlit wetlands has repeatedly been marveled at, written about, and also exploited. A popular public image is of herds of lechwe plunging through the shallows of a central African wetland – as depicted on the cover of *Okavango: Sea of Land, Land of Water* (Johnson & Bannister 1977). Lechwe and kobs have become firmly established as flagship species for conservation. This began before the Second World War in the then Northern Rhodesia, where the colonial Game Management authorities were concerned over the future of the black lechwe around Lake Bangweulu, a concern heightened in the 1950s with the rapid decline in populations of Kafue and black lechwe. A major catalyst in conservation was the activities and advocacy of an NGO, the Game Preservation Society of Northern Rhodesia (that later became the Wildlife Society of Zambia). Indeed, the official journal of the Wildlife Society of Zambia was named "Black Lechwe", and the research journal of the Zambian Department of National Parks was named *The Puku.* This focus on these single species symbolized concern about the future of Zambia’s formerly rich wildlife.

3.1.1 **Geographical and taxonomic scope**

The focus of this review is on the evolution, diversification and current status of the Reduncini. This is the crux of the knowledge of a taxon regarding properties of biodiversity. With respect to the attributes of biodiversity knowledge, information pertaining to evolutionary biology and biogeography has been reviewed rather than the larger assemblage of detailed information published about the behaviour and ecology of the Reduncini in the Zambezi Basin and elsewhere in Africa.

The extent of the Zambezi Basin recognized in this review extends beyond its modern watersheds. It includes the entire modern drainage of the Zambezi as well as the Okavango Delta and its tributaries; and the Bangweulu and Mweru basins (northern Zambia). It also considers the Upemba and Rukwa depressions in the Democratic Republic of Congo (DRC) and Tanzania, respectively. This region encompasses much of Malawi, eastern Angola, southern Shaba Province of the DRC, central Mozambique, northeastern Botswana, and northern Zimbabwe. All of Zambia is included. This coverage is essential to account for the evolution of the Zambezi and neighboring drainage systems, and the biota therein, which have changed considerably over the past five million years since the Miocene.

The Bohor reedbuck (including a total of seven subspecies recognized by Ansell 1971) is excluded from this review because there is no evidence of the species occurring in the Zambezi Basin, nor in Malawi or Zambia, but it does extend into the Rovuma Valley of northern Mozambique and perhaps further south. Mountain Reedbuck, *R. fulvorufula*, does not occur within the Zambezi Basin; three subspecies have been described, the populations of which are restricted to suitable mountainous habitat in southern Africa (*R. f. fulvorufula*), north-east Africa (*R. f. chanleri*), and a relict population on Mount Adamua in Cameroon (*R. f. adamuae*). The Nile lechwe, *Kobus megaceros* is not specifically reviewed given its restricted distribution in southern Sudan and adjacent western Ethiopia. The Kob, *K. kob,* formerly widely distributed across the Guinean savannas of North Africa, is excluded for a similar reason. It is pertinent to note that *K. kob* (of which several allopatric populations have been described as subspecies) in equatorial Africa and the northern, Guinean savannas is very closely related to the pukus (*K. vardoni* and *K. senganus*), whose distribution centres on Zambia.

3.2 PHYLOGENETIC ORIGINS AND PALAEONTOLOGICAL BACKGROUND

3.2.1 Taxonomic preamble

With the exception of painstaking palaeontological research into various fossil beds in Africa (for example, Gentry 1990, Vrba 1979, Vrba *et al.* 1994) the study, and most especially resolution, of the systematics of reduncine antelopes has not kept pace with more utilitarian attention to their exploitation and conservation. Comparatively little has been published about the taxonomic status of the many described populations of the Reduncini, and the few available tend to focus on the lechwes (Ansell 1964, 1971, Ansell & Banfield 1980, Barclay 1933). Apart from Vrba *et al.* (1994), no systematic research of the Reduncini has employed the modern techniques and philosophy of modern systematics. This is unfortunate. It is difficult to state unequivocally how many species of reduncine antelopes occur within the Zambezi Basin or within Africa overall. Lack of data, and more especially its synthesis by modern phylogenetic systematists, is one cause of this deficiency. Another allied reason is that an objective concept of the species (one which objectively interprets mammalian diversity) has yet to be applied to the Reduncini, and indeed most other mammals.

The establishment of objective criteria to identify a reduncine species is obviously a prerequisite to study any aspect of its biology and generate reliable knowledge. Some discussion is devoted to this problem, given its impacts on scientific knowledge and biodiversity conservation. An underlying premise of this review is that the study of the ecology and behaviour of any aspect of an organism's biology must be founded on accurate taxonomy. Such taxonomy must seek to "carve nature at its historical joints" and discover species and their historical relationships – to objectively identify real species, that is relevant evolutionary products of diversification. This procedure must unearth cryptic species yet avoid descriptions of artificial taxa. It is precisely this knowledge that is a prerequisite to frame scientifically-sound knowledge to conserve organismal biodiversity (Cracraft 1997, Dimmick *et al*. 1999, Soltis & Gitzendanner 1999). Indeed, the application of a more objective perspective on what species are (their ontology) confers profound implications on how the Reduncini are classified, and this in turn provides important lessons to the understanding of biogeography and biodiversity in the Zambezi Basin. The Reduncini constitute an important case study for the scientific study of biodiversity and its conservation in Africa and elsewhere. The perspective gained from understanding reduncine diversity is especially relevant to wetlands.

3.2.2 **Evolution**

The Reduncini evolved over 15 million years ago. The oldest known fossils are 11 million years old from East Africa. The group formerly occurred in Asia, as of 5 million years ago. It has been suggested that this dispersal out of Africa corresponded with mesic conditions that facilitated their dispersal down the Nile Valley. Diagnostic characters of reduncine antelopes are transverse ridges on their horns (only present in males), a large maxillary tuberosity, comparatively small cheek teeth, and no less than three other diagnostic characters of the lower and upper molar teeth (Gentry 1990, Kingdon 1982).

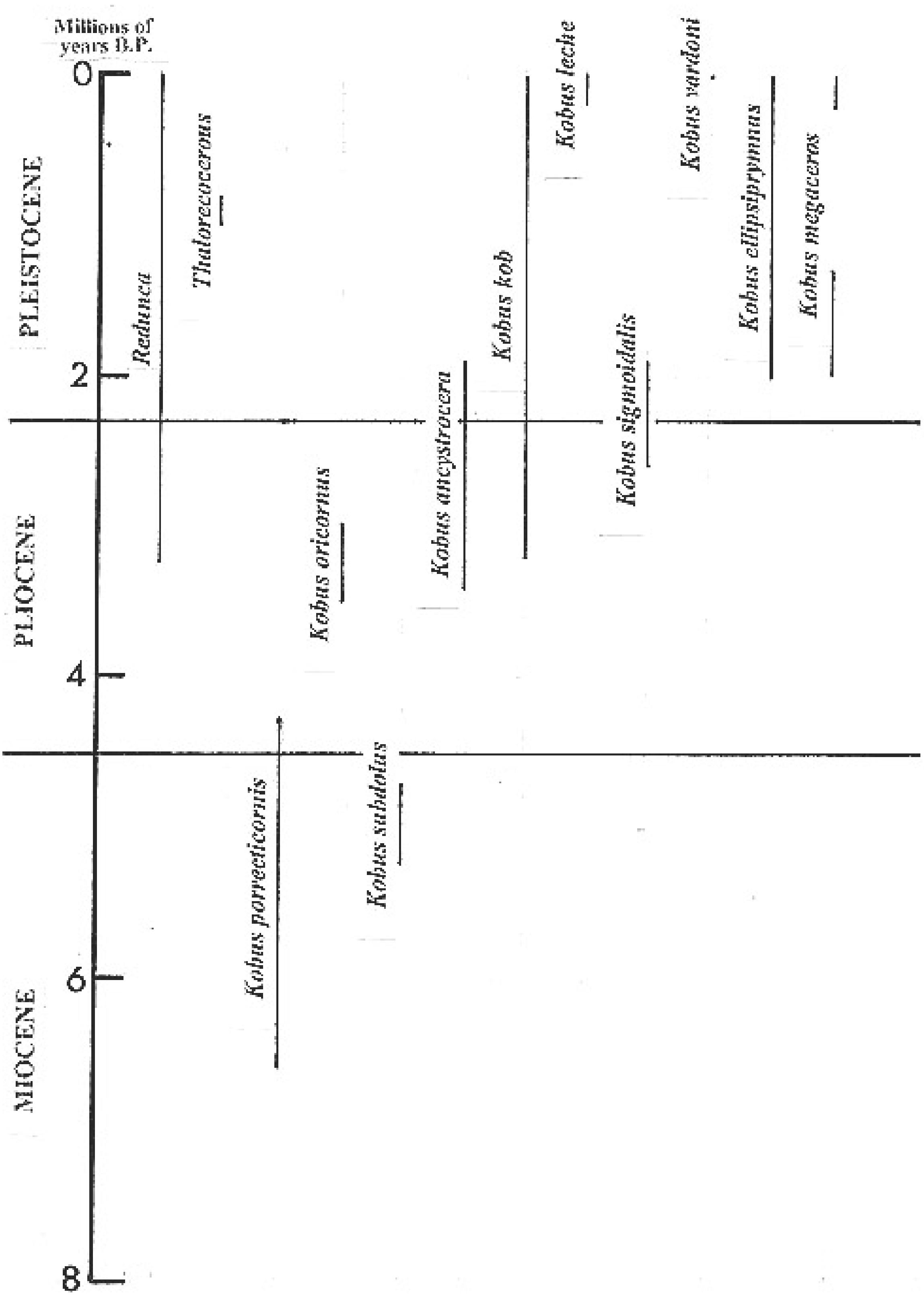
Reduncine fossils have been collected from many of Africa's fossil beds in Quaternary and Tertiary formations in Kenya, Ethiopia, Tanzania and South Africa. The earliest known fossils are assigned to *Kobus porrecticornis* (7-4.5 Million years ago [Mya]) and *K. subdolus* (5 Mya). A pulse of diversification of *Kobus* occurred in the late Miocene and early Pleistocene (Figure 3.1; Gentry 1990). Noteworthy records are that the lineage of "waterbuck", *K. ellipsiprymnus* and "Ugandan Kob", *K. kob* can be traced back to 2 and 3 Mya, respectively. The fossil reduncines assigned to "Red lechwe" *K. leche* and "Nile Lechwe" *K. megaceros* are far more recent – tens of thousands of years old.

The genus *Redunca* appears over 3.0 Mya. No less than three sympatric species have been discovered from the dolomite strata of northern South Africa, including examples of the extant *arundinum* and *fulvorufula*, and the extinct *R. darti* (McKee 1995). Exploration of geological formations likely to hold fossils in Zambia and northern Zimbabwe has yet to be carried out.

Nevertheless, the identity of the immediate ancestors of the Reduncini and their extant relatives is unclear. This uncertainty is evident in how inferences of higher level phylogeny have influenced classifications of the Bovidae. Vrba (1979) concluded that the Reduncini diverged from a clade which ultimately formed the Neotragini (stenbuck, suni, royal antelope and grysbucks). This treatment was followed by Meester *et al*. (1986) and Skinner & Smithers (1990). Neotragines are considered to be primitive antelopes, as exemplified by *Raphicerus sharpei* (Sharpe's grysbuck). Evidence for this relationship can be seen in puku, which possess a vestigial preorbital gland common to all neotragines. Additional evidence is represented in the ontogeny of horn growth in waterbuck, lechwe and reedbuck. Primitive swept back horns (a shared neotragine trait) in juveniles proceeds to the large, lyrate horns of the adult reduncine. Indeed, reduncine evolution has involved elaboration of horns and scent glands (Kingdon 1982).

In a different taxonomic treatment, Gentry (1990) placed the tribe Reduncini alongside its sister tribe Hippotragini (oryx, sable, roan and allies) to form the subfamily Hippotraginae, but acknowledged understanding of bovid relationships at this level (above the genus) to be poor. One derived character which Gentry considered shared among these antelopes is the enlarged basioccipital (where an enlarged longus capitis muscle inserts on the skull). This adaptation permits powerful and rapid downward head movements, and occurs in alcelaphines, hippotragines and reduncines: nevertheless, as Kingdon (1982)

Figure 3.1. Geological time scale showing the approximate durations of certain morphospecies of the Reduncini as established from the African fossil record since the late Miocene (modified from Gentry 1990).



argues, its possession does not necessarily infer common ancestry. Separate fossils from Langebaanweg, South Africa and Pinjor, Siwaliks, even suggest that Reduncini as currently recognized might be paraphyletic. In this respect, Gentry (1990) notes that the genus *Ourebia* (currently recognized as a neotragine) possesses certain characters more typical of reduncines than neotragines. This is apparent in the considerable similarity of the subauricular glands of oribi, *Ourebia ourebi*, and mountain reedbuck, *Redunca fulvorufula* (Kingdon 1982, Vrba *et al*. 1994). The inclusion of *Ourebia* in the Reduncini is also supported by dependence of oribi on mesic habitats and their need for surface water, and their loud whistling call reminiscent of reedbucks. Conversely, most other neotragines are adapted to dry forests, savannas and deserts, with one species occurring in moist forest. Given its resemblance to neotragines, but also reduncine affinities, the extant *Ourebia ourebi* could be a primitive reduncine.

3.2.3 **Adaptation to aquatic habitats and environmental disturbance**

The lechwe are unique among the reduncine antelopes in being able to live permanently in wetlands. Their adaptations represent extreme specialization. Kingdon (1982) has suggested that a neotragine ancestor of the Reduncini occupied tropical valleys and its descendants diversified to exploit valley grasslands, followed by adaptation to aquatic conditions in mesic environments. Nevertheless, wetlands are characterized by frequent disturbance, and the exploitation and associated specialization required to exploit wet grasslands exposed reduncines to such disturbances as diseases, parasites, fluctuating water levels associated with climatic extremes (floods to droughts), fires and predation.

Very recently (on a palaeoecological time scale), humans have become a dominant agent of disturbance in reduncine habitats, either through direct depredation, or habitat modification (especially through fire and hydrological developments), or by competition with livestock. However, disturbances has not all been caused by humans. Climate and tectonic-driven changes to wetlands appear to have had a major impact on reduncine diversity. These have caused dramatic and recent changes in the distribution and diversification of reduncine antelopes. In particular, comparatively recent disturbances (on an evolutionary time scale) to Zambezian wetlands are of considerable interest. The details and implications of these phenomena are considered in the final section of this review.

Some even more recent changes in distribution have also occurred. Fluctuations in the distribution of *K. leche* in northern Botswana since the mid-19th century exemplify the susceptibility of these antelopes to habitat change. David Livingstone during his search for Lake Ngami in 1849 collected the first specimens of *Kobus leche* known to science from its vicinity (Spinage 1994), while Andersson (1856) recorded hundreds of this species on the Taoghe Delta on the edge of Lake Ngami. This area was then perennial swamp. Today, the landscape supports open, semiarid grassland and the Taoghe river is dry. The lechwe of Lake Ngami are extinct. The nearest lechwe only occur in the Okavango, over 60 km to the north (Smithers 1971, Spinage 1994). This example illustrates how vagaries of changes in habitats have modified the distributions of these antelopes within very short time periods.

3.3 SOCIAL ORGANISATION AND BEHAVIOUR

3.3.1 **Sociality and adaptation to open, mesic habitats**

The social organization of nearly all currently recognized species of reduncines has been well studied, and is characterized by high levels of competition amongst males for mates. Only a minority of males secure territorial tenure and thus matings. These social systems have evolved in response to the comparative uniformity of the grassland and aquatic habitats exploited by reduncines, where high densities of antelopes congregate (Nefdt 1995, 1996, Rosser 1987). All reduncine antelopes live in herds, which reach their highest extremes in density and size in the kobs and lechwes. The behavioural organization of lechwe (Nefdt 1995, 1996, Thirgood *et al.* 1992), waterbuck (Hanks *et al.* 1969, Herbert 1972, Melton 1978, Spinage 1982), reedbuck (Howard 1986a, 1986b) and puku (de Vos 1965, de Vos & Dowsett 1966, Rosser 1987) have been studied in detail, focussing especially on social organization and mating systems.

The lek breeding system – based on territorial defence where only a minority of dominant males secure matings – are exemplified in certain lechwe, puku and kob. Significantly, the first record of lek breeding in a mammal was recorded in the Reduncini (*K. kob*, Buechner 1961). These social systems have evolved in response to high densities of antelopes in specific habitats. Territorial and other disputes between individuals are frequent and follow highly ritualized behavioural repertoires (Leuthold 1977). Lechwe exhibit significant diversity in breeding systems: *K. kafuensis* and *K. leche* (in the Linyanti) defend and mate on leks, but *K. smithemani* does not (Thirgood *et al.* 1992). These social systems of reduncines are correlated with their morphological adaptations. Chief amongst these are the scent glands and robust horns. Scent marks are important in denoting information about reproductive and social status (Kingdon 1982), thus the social organization of reduncines is dominated by olfactory cues. All reduncines have a strong musky odour from secretions of the sebaceous glands – waterbuck (*K. ellipsiprymnus*) are noted for their strong "turpentine-like" odour, and strong odours also characterize reedbuck and lechwe. It appears that reduncine scents are species-specific and are involved in recognition of conspecifics in territoriality and mate choice. A semiochemical function of scent marks has been demonstrated for two species of lechwe (Deustch & Nefdt 1992). A diversity of specialized scent glands in reduncines include subauricular, pedal and inguinal glands, and the scented fur is maintained by an oily secretion into the fur from the sebaceous glands (Kingdon 1982). Territorial, sexually active puku males have a glandular secretion on the neck (Rosser 1987).

Only male reduncines have horns. The evolutionary trend has been toward enlargement of horns, which has reached its extreme in lechwe and waterbuck. Large horns function as signalling devices and are used in ritual sparring among males over status, territories and mates. A key adaptation has evolved to allow the powerful and violent head movements of males, manifest in the thick necks of puku, lechwe and kob. Sexual dimorphism renders this trait especially noticeable in males. The conspicuous evidence of this adaptation has been hypertrophy of the longus capitis muscle underlying the spinal column, which contracts the neck and lowers the head. Enlargement of this muscle is associated with larger processes of the cervical vertebrae and the basioccipital processes at the base of the reduncine skull (Kingdon 1982).

3.3.2 **Ecological relevance**

A common trait of Reduncini is close association with aquatic habitats, and all are dependent on surface water. Lechwe, in particular, have a predilection for floodplains, a dependency that appears to be physiological and is presumably primitive in its evolution, being manifest throughout extant reduncines (Kingdon 1982) including Mountain Reedbuck, *Redunca fulvorufula* (Smithers 1971).

Several authors (Schuster 1976, 1980) have emphasized the impact of lechwe on floodplains, especially the Kafue and Bangweulu. Here, dense concentrations of lechwe represent an extreme manifestation of the phenomenon.

The dominant role of reduncine antelopes in the ecology of aquatic landscapes in Africa has been largely inferred. Williamson (1981) notes that grazing by lechwe in the Linyanti has had a major impact on the sward, reducing large areas to closely-cropped lawns. Apart from calculations of biomass, there has been no quantitative demonstration of the impacts of these antelopes on nutrient flux or effects on other populations (invertebrates, fishes and waterbirds). It is equally valid to infer that the specific habitat selection by reduncine antelopes will have a marked impact through their trampling of the substrate. This would especially apply to seasonal concentrations of these antelopes when breeding. In this respect, *K. smithemani* and *K. kafuensis* appear to hold a keystone role in certain aquatic landscapes, such as the Bangweulu and Kafue floodplains, due to trampling of the floodplain and participating in nutrient cycling. The biomass of Kafue lechwe has been recorded as the highest known carrying capacity for large mammals (11,000 kg/km^2), although this figure fluctuated with seasonal flooding regimes (Schuster 1980).

3.4 POPULATION STATUS AND HISTORICAL DECLINES

This section summarizes the status of Reduncini in significant areas within the Zambezi Basin, with a focus on the principal wetlands. The definitive source is East's (1989a, 1989b) multi- authored survey of the status and conservation of antelopes in southern and south-central Africa, which includes country reports and a regional review. Where possible, evidence for changes within the basin is included. The earliest records are from the writings of David Livingstone, who explored the Zambezi and some of its tributaries in the mid-19th century. Important records have been summarized by Benson (1974). Additional information can be obtained in the writings of later explorers and hunters, notably F.C. Selous (Selous 1881, 1908).

3.4.1 **Barotseland**

Populations of waterbuck and lechwe have declined within the region (Figures 3.2 and 3.3), as concluded from historical records since the early 20th century (Ansell 1960a, 1978). Waterbuck do not occur west of the Zambezi. Reedbuck appear widespread where human depredation is not excessive (East 1989a).

3.4.2 **South eastern and central Angola**

Populations of red lechwe and waterbuck extend from the Upper Zambezi valley within western Zambia into southern Angola (Figures 3.2 and 3.3). The status of waterbuck along the Cubango, Luiana and Okavango (Kavango) rivers is unknown, but they are suspected to have declined. Given the decline of the Namibian population, the overall status of this population (believed to be *penricei*) could be precarious. It is noteworthy that an isolated population of puku occurs in the Luando National Park in C Angola. Red lechwe occur along the Zambezi in E Angola and the Cuando in the south east within the Luiana and Mavinga Reserves (East 1989a). Red lechwe are considered rare in Angola (East 1989a) and their current status cannot be established. This situation is unsettling, as the taxonomic status of these populations (especially the widely separated populations of the Cubango, Luiana and Kavango rivers) is unclear.

Figure 3.2. Distribution of two species of waterbuck (*Kobus crawshayi, K. ellipsiprymnus*) in the Zambezi Basin (after Ansell 1978, Ansell & Dowsett 1988, East 1989a,b, Griffin & Joubert 1991, Rodgers 1984, Skinner & Smithers 1990). Distributions of *K. kondoensis* and *K. penricei* are not mapped in detail, being subject to future biogeographical and phylogenetic refinement. Hatched areas depict approximate distributions summarized by East (1989a,b) where specimen data could not be located. Open symbols are localities of historical occurrence.

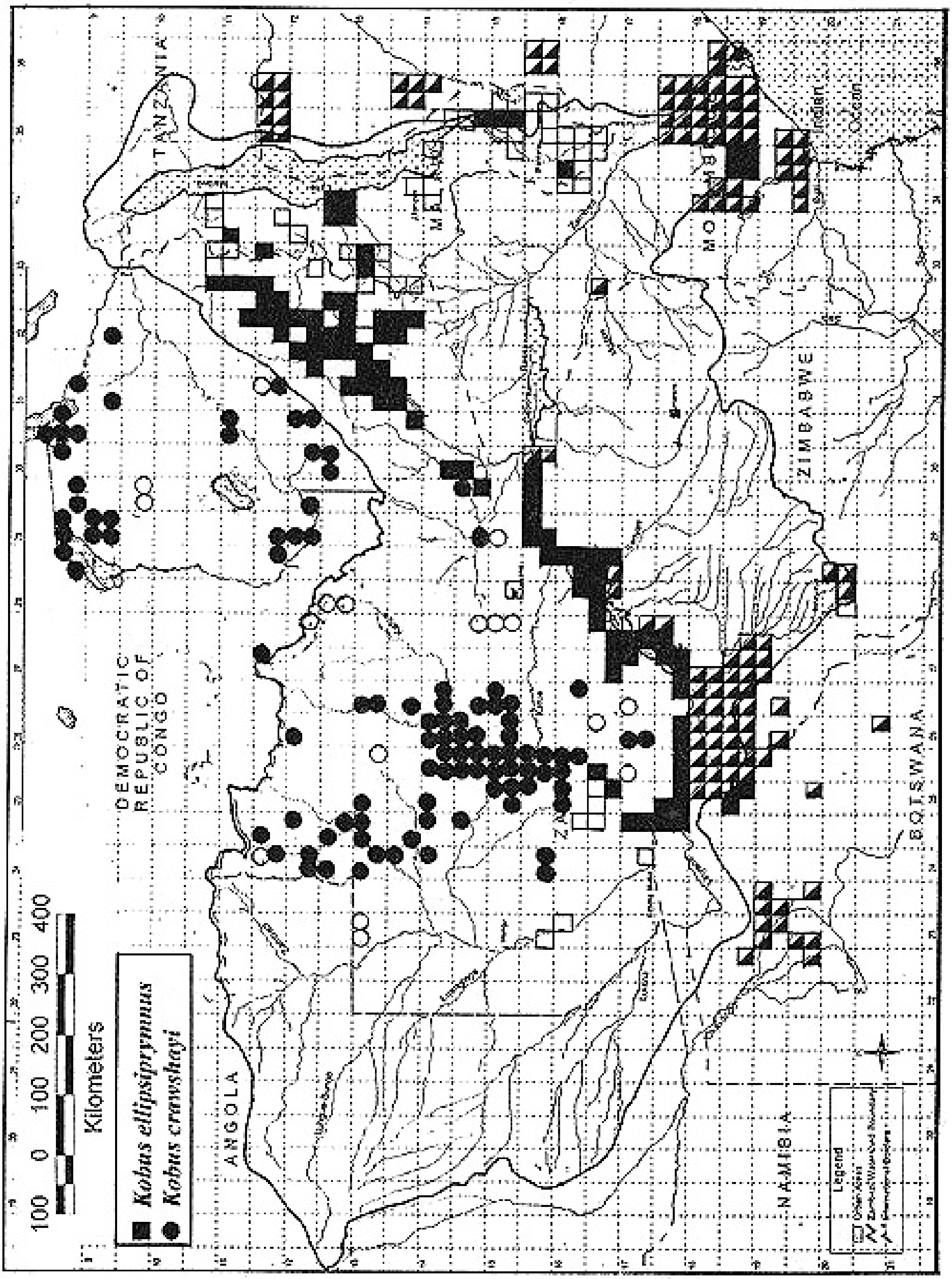
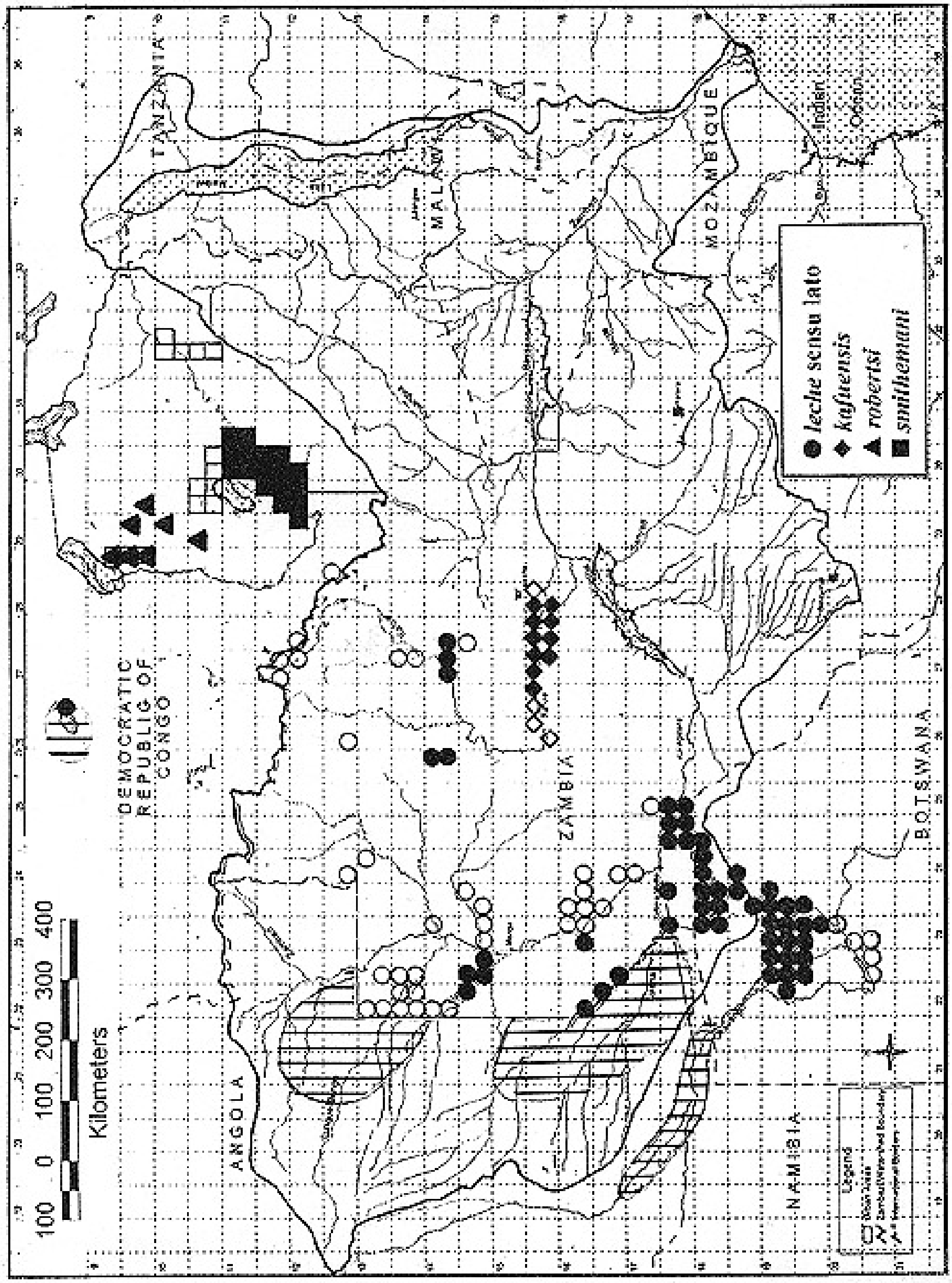


Figure 3.3. Distribution of four "subspecies" of lechwe (*Kobus l. leche* sensu lato, *K. l. kafuensis, K. l. robertsi*, *K. l. smithemani*) in the Zambezi Basin (data from Ansell 1978, Ansell & Dowsett 1988, Dollman 1921, East 1989a,b, Griffin & Joubert 1991, Smithers 1971, Skinner & Smithers 1990). Distributions of outlying allopatric populations of *K.* "*leche*" are also depicted which include *K. notatus* and *K. amboellensis*. Hatched areas depict approximate distributions summarized by East (1989a,b) where specimen data could not be located. Open symbols are localities of historical occurrence.



3.4.3 Caprivi and Chobe/Linyanti

Overall, reduncine populations have declined in the western Caprivi and certain species apparently occur marginally (East 1989a). Over the past 100 years, puku have declined greatly in the eastern Caprivi (East 1989a, Smithers 1983), and their status is marginal and precarious in Namibia (Figure 3.4). As of the 1980s, a relic population of approximately 50 animals persisted on the Chobe floodplain in Botswana (East 1989a, Smithers 1983). F.C. Selous first visited the Puku Flats in 1874, when puku were very numerous, but they were greatly disturbed by dense settlement in 1876 by refugees following political turmoil in Barotseland. They have never recovered from this human impact (Dollman 1921). Puku also declined to extinction on Impalila Island in the Caprivi after its settlement in 1958 (Child 1968).

It has been suggested that the total population of reedbuck within Namibia is approximately 50 individuals (East 1989a). Griffin & Grobler (1991) noted sightings of waterbuck in the eastern Caprivi between 1983 and 1987 but none since, and record a decline of waterbuck along the Kwando floodplain. Red lechwe are the exception. As of the late 1980s, a population of over 4300 occurred in the eastern Caprivi, and 150-200 in the western Caprivi. It has been estimated that several thousand red lechwe occur in the Linyanti area of Botswana, and these migrate seasonally into the Chobe floodplain (Williamson 1981, East 1989a).

3.4.4 Okavango Delta

Populations of reduncine populations appear healthy where human settlement has not excluded or depleted their populations. This includes stable populations of waterbuck (the Botswana national population of 900 is largely concentrated within the Okavango), reedbuck (small) and red lechwe. Over 20 000 red lechwe are estimated to occur in the Okavango.

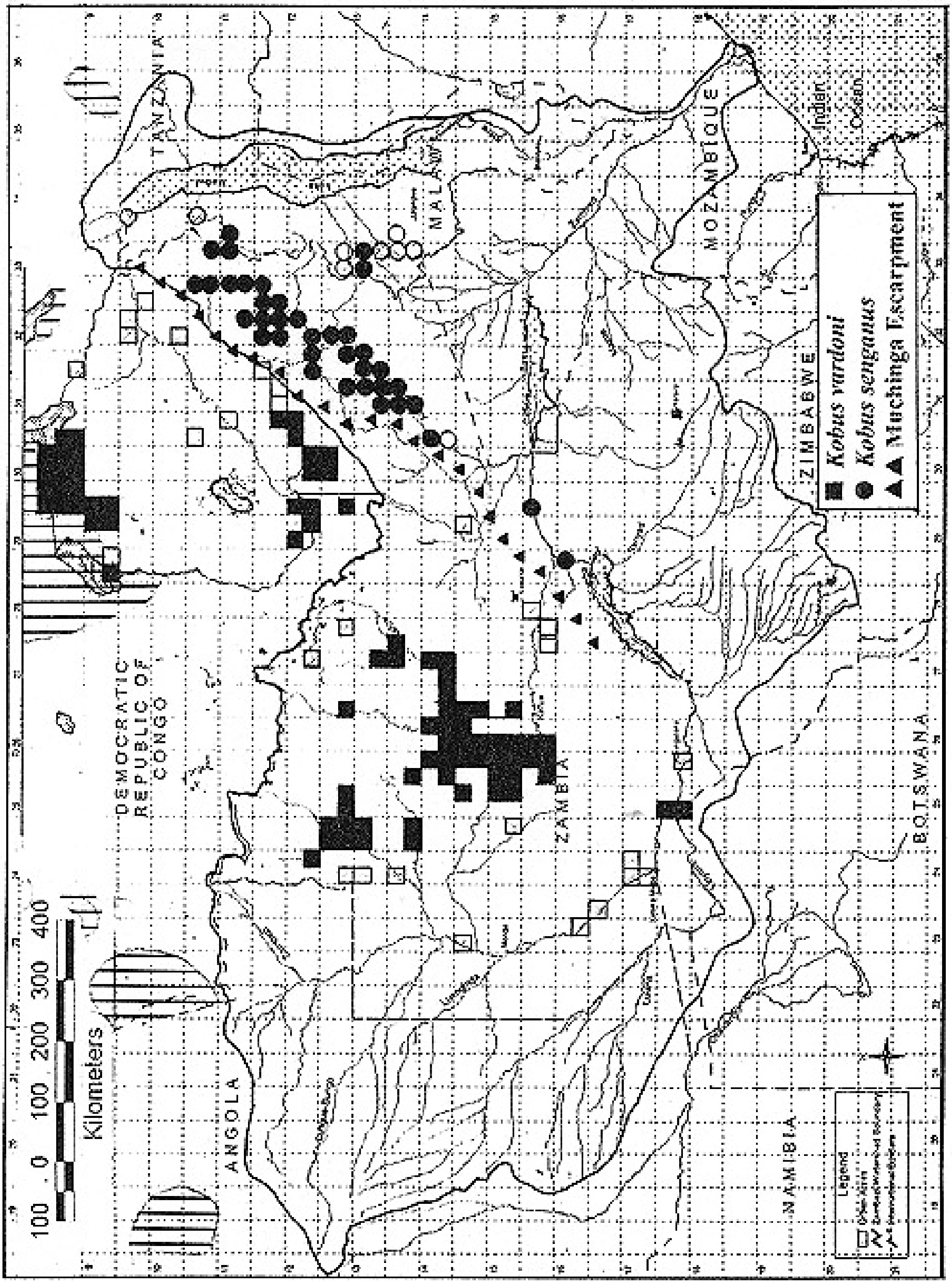
Smithers (1971) discusses the local extinction of lechwe from Lake Ngami since the last century. They were not encountered by the Vernay-Lang Kalahari expedition which crossed Lake Ngami in May 1930, and which went on to collect 10 red lechwe from the vicinity of the Kwaai River from 6-28 May 1930 (Hill 1942).

3.4.5 Bangweulu Flats

Black lechwe formerly occurred in their hundreds of thousands in the Bangweulu Basin in the early part of the 20th Century (Allen 1963, Ansell 1978, Bell & Grimsdell 1973, Howard *et al.* 1984, Hughes 1933, Letcher 1910, Thirgood *et al.* 1994). The biology and status of black lechwe and their environment has been the subject of a comprehensive report (Grimsdell & Bell 1975). The population has since undergone a dramatic decline both in its range and abundance. This extirpation elicited considerable concern and much subsequent study.

The major cause of the decline of *K. smithemani* has been accelerated human depredations – much of it driven by commercial poaching to supply protein demands on the Copperbelt. This commercialization of exploitation changed what had previously been a localized economy of subsistence hunting by the resident people (Batwa, Baunga and Bisa tribes). Modern technology – in the form of firearms for hunting, and vehicles for transportation – aided and accelerated these depredations (Grimsdell & Bell 1976). An added mortality agent was predation by the abundant lion, *Panthera leo*, population in the Mpika District of Lake Bangweulu in the mid-20th century. Following a drastic decline in the prey populations of the miombo savannas surrounding the wetland, these lions modified their hunting behaviour to a semi-aquatic existence, successfully hunting Black Lechwe (Allen 1963).

Figure 3.4. Distribution of two species of puku (*Kobus senganus* and *K. vardoni*) in the Zambezi Basin (data from Ansell 1978, Ansell & Dowsett 1988, Griffin & Joubert 1991, Rodgers 1984, Skinner & Smithers 1990, Smithers 1971). The taxonomic status of the isolated populations in Tanzania are not known. The cross-hatched line approximates the Muchinga Escarpment. Hatched areas depict approximate distributions summarized by East (1989a,b) where specimen data could not be located. Open symbols are localities of historical occurrence.



It is noteworthy that an abnormally high flood after 1936 significantly depleted numbers of *K. smithemani*, which dropped from at least 150,000 to 40-60,000 individuals. The raised water level squeezed the population into the remaining habitat, where they were also more susceptible to intense hunting that began with poaching for meat rations during the Second World War, and was commercialized thereafter. Numbers declined to about 16,000 in 1969.

This episodic flooding illustrates the comparative susceptibility of a large herbivore with specific habitat requirements, although in the case of lechwe it is offset by their high reproductive potential. Grimsdell & Bell (1976) estimated a population increase approximating 25% from 16,000 in 1969 to 30,000 in 1976. Based on repeated censuses from 1988 to 1991, the latest report (Thirgood *et al.* 1994) records the population of *K. smithemani* in the southern Bangweulu to have recovered to approximately 30,000 individuals. It remains threatened by poaching and improved access to the area (especially in the west). Thirgood *et al.* (1994) emphasize the importance of securing the Chimbwi Plain as a dry season refuge for the population.

3.4.6 **Lake Mweru**

I have not been able to obtain reports which focus directly on the reduncines occurring on the margins of Lake Mweru and its tributaries. This is unfortunate. Ansell (1974) paid some attention to the taxonomic position and status of the Luena lechwe, *K. robertsi* – concluded to be extinct (Figure 3.3).

3.4.7 **Busanga Flats, Kafue National Park**

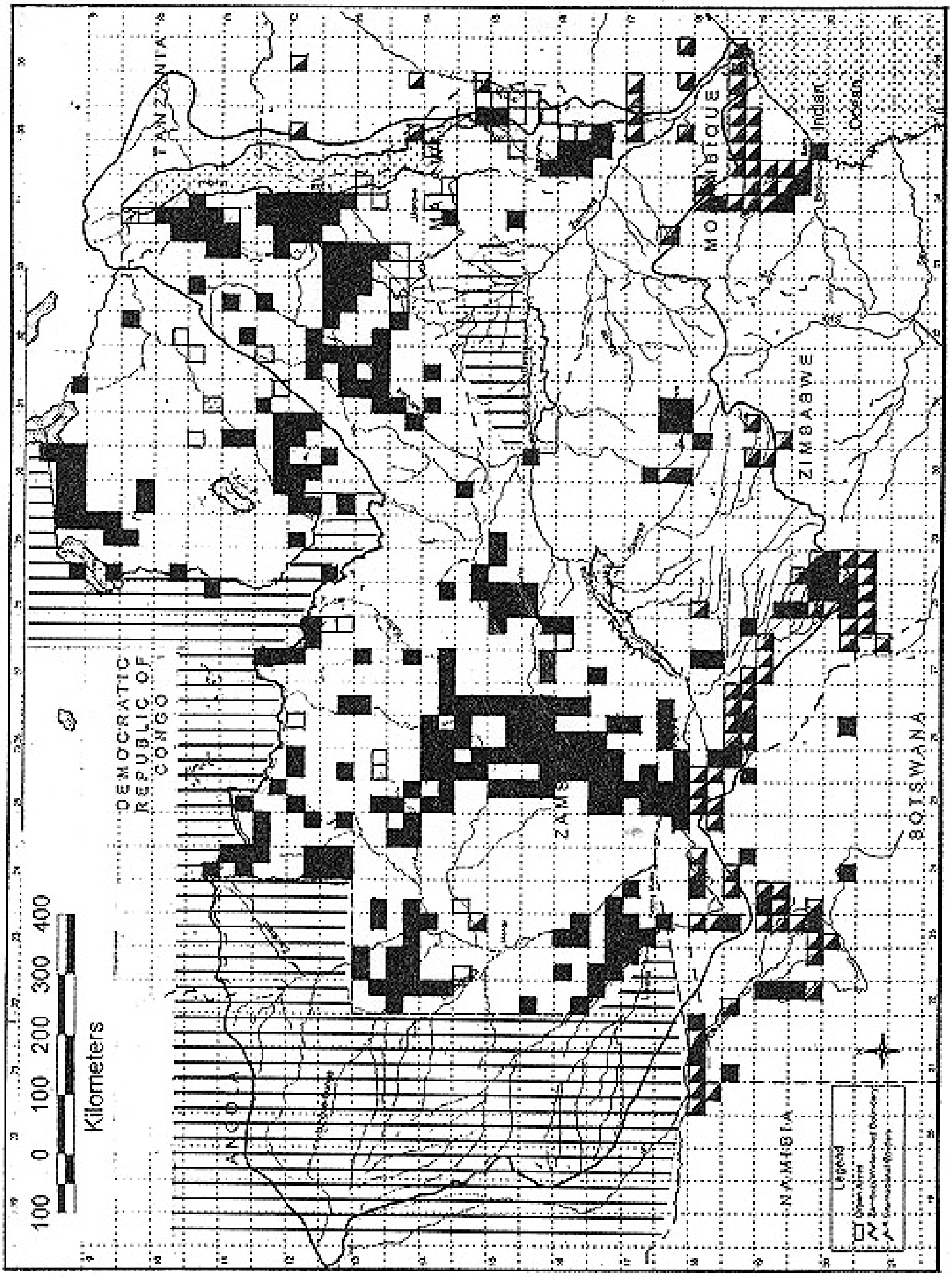
Rapid recovery of lechwe populations has been recorded in the northern region of the Kafue National Park (Figure 3.3), where the red lechwe population had recovered from an estimated 71 animals in October 1948 to 1163 in July 1971 (Grimsdell & Bell 1972). The most recent report estimated that this population numbered 3400 in 1985 (Howard & Chabwela 1987). The latter census covered both wet and dry seasons.

3.4.8 **Kafue Flats**

The Kafue Flats are of significant conservation status as the endemic Kafue lechwe is entirely restricted to this locality (Figure 3.3). The formerly widespread population is now restricted to Blue Lagoon and Lochinvar National Parks. Construction of hydroelectric schemes (centered on the Kafue Dam) were predicted to cause major disruptions to the Kafue Flats and its biota. Alteration of the flooding regime was particularly expected to affect Kafue lechwe by impacting on their social behaviour (Schuster 1980). Numbers declined by 50% between 1972 and 1981, but their total distribution has not changed significantly. Long term affects of this acute hydrological perturbation on the Kafue biota have still to be established (East 1989a, Sheppe 1985). The leks of Kafue lechwe are restricted to a remarkably small area (Nefdt 1996). Nonetheless, the reproductive seasonality of Kafue lechwe has since changed with a modification in timing of floods released from impoundments upstream. The primary cue that initiates mating appears to be rising flood waters: young born seven months later benefit nutritionally from exposed forage as waters recede from the floodplain (Nefdt 1996). Nefdt (1996) records that although Kafue lechwes mate and conceive throughout the year, a significant peak in births occurs in periods of maximal forage availability (over a period of one to two months), especially when water levels on the floodplain are receding and exposing nutritious forage.

A recent visit to Lochinvar National Park in October 1999 and discussions with local authorities revealed that commercial poaching of *K. kafuensis* is rife, especially in Blue Lagoon National Park, where depredations are unsustainable.

Figure 3.5. Distribution of southern and northern reedbuck (*Redunca arundinum* and *R. occidentalis*) in the Zambezi Basin (data from Ansell 1978, Ansell & Dowsett 1988, East 1989a,b, Griffin & Joubert 1991, Skinner & Smithers 1990). No attempt has been made to distinguish between distributions of the two populations. Hatched areas depict approximate distributions summarized by East (1989a,b) where specimen data could not be located. Open symbols are localities of historical occurrence.



3.4.9 Lower Shire and Malawi

Waterbuck and reedbuck (Figures 3.2 and 3.5) originally occurred throughout the Lower Shire in suitable habitat (Ansell & Dowsett 1988). These populations were virtually extirpated with widespread settlement by rural human populations and associated development. They only persist in the Liwonde and Majete Reserves. Reedbuck still occur in certain protected areas, notably Nyika National Park (East 1989a). Elsewhere in Malawi, waterbuck only survive in protected areas such as Liwonde National Park and Nkhotakhota and Majete Game Reserves. It appears to be declining in the Kasungu National Park and is believed extinct in the Vwaza Marsh Game Reserve (Ansell & Dowsett 1988). Puku have always had a very restricted distribution in Malawi (Ansell & Dowsett 1988, Lyell 1913; Figure 3.4).

3.4.10 Middle Zambezi Valley

Healthy populations of waterbuck persist within the protected areas across the middle Zambezi Basin, including Matusadona, Mana and Zambezi National Parks, and where human settlement has not reduced their numbers in suitable habitat (East 1989a). Reedbuck appear to be absent from large parts of the middle Zambezi Valley, and occur locally in northwestern Zimbabwe upstream of Victoria Falls. Reedbuck appear to have declined within the region, possibly due to increased aridity. Large numbers of waterbuck and reedbuck were extirpated in the Sebungwe and Urungwe regions of Zimbabwe during Tsetse Control operations into the 1960s – a total of 16,644 reedbuck and 10,371 waterbuck were shot between 1933 and 1958 – the majority from the Middle Zambezi Valley. The falling proportion of these reduncines' contribution to total kills through this period suggests a significant impact on the population (Child & Riney 1987).

3.4.11 Zambezi Delta and Gorongosa

Important populations of reedbuck and waterbuck persisted in Sofala Province and southern regions of the Zambezi Delta into the 1980s, but experienced major depredations thereafter. The northern region of Sofala Province (including Gorongosa and Marromeu) was estimated to support 90% of the vulnerable waterbuck population in Mozambique (East 1989a).The first census in 1968 suggested a population of 4300 waterbuck, concentrated in south and central Marromeu (Tinley 1969). A survey in June 1994 revealed that intact populations of reedbuck occurred in Gorongosa National Park, but comparatively few were seen in Marromeu. Previously, the waterbuck population in Marromeu was of the order of 50,000 in the late 1970s, but the 1994 census estimated that only between 33 and 230 animals had survived (Cumming *et al.* 1994). Given the localized, apparently allopatric range of this waterbuck population (Figure 3.2), its taxonomic status requires investigation. Originally, reedbuck were widespread and common where human depredations are not excessive, with Marromeu-Gorongosa being the stronghold of the species in Mozambique. They also appear to have benefited from a partial drying out of the Marromeu floodplain during the 1980s. Chambal (1989) suggested that very few reedbuck (21) existed in Marromeu in 1988, and Cumming *et al.* (1994) estimated the total population of central Marromeu at a meagre 10 individuals. These figures appear to be underestimates as Anderson *et al.* (1990) estimated the population of the ecotone and floodplains (admittedly a larger area) at 260. Nonetheless, reedbuck have declined catastrophically since the 1970s. Recent catastrophic crashes in these reduncine populations (and other large mammals) have obviously created a conservation crisis in the region. Most recently (July 1999), the population of reedbuck appears to be recovering.

3.5 TAXONOMY AND STATUS OF REDUNCINE POPULATIONS

I have attempted to identify each significant population of the reduncine antelopes that have been recognized by taxonomists at the subspecific level or higher, and/or have been recognized as discrete populations with definite geographical boundaries. Thus the following species accounts apply the species category loosely and would be better labelled "population accounts". They provide short reviews of the taxonomy and distribution of each discrete population (selected mainly on subspecific criteria), with a synopsis of the current status of each. The accounts form an introductory framework to review the diversity of the Reduncini in more detail to elucidate a more accurate taxonomy. Conservation status is derived from East (1989a, 1989b).

I place particular emphasis on the evolutionary distinction of a species. This recognizes most allopatric populations as full species, and is in direct conflict with the traditional orthodoxy of the Biological Species Concept (BSC) with its firm reliance on reproductive isolation. A significant departure from this orthodoxy is that the concept of subspecies is not applied (see Cracraft 1997 for further discussion). The differences, and especially the implications and impacts for conservation, of this two philosophies are important, and are discussed in detail in the next section.

REEDBUCK

Southern Reedbuck, *Redunca arundinum*

Taxonomy and Distribution

R. arundinum is sympatric with the Bohor reedbuck, *R. redunca* in W Tanzania in the drainage of the Ugalla and Moyowosi rivers. Key characters distinguishing these species include the number of inguinal pouches, pelage and horn shape (Ansell 1971).

Two subspecies were recognized by Ansell (1971), who notes that *thomasinae* Sclater, 1900 (from the Songwe River separating Tanzania and Malawi) has priority over usage of *occidentalis*, should the northern race prove separable:

R. a. arundinum (Boddaert,1785) includes *eleotragus* Schreber,1787; *coerulescens* Link,1795; *arundinacea* Bechstein,1799; *cinerea* Bechstein,1800; *isaellina* Afzelius,1815; *oleotragus* Desmoulins,1822; *multiannulata* Fitzinger,1869; *caffra* Fitzinger,1869; and *algoensis* Fitzinger, 1869.

The southern reedbuck was formerly widely distributed in the Zambezi Basin in all the riparian states, wherever suitable habitat occurs.

Status

Status of this widely distributed species varies from Vulnerable to Least Concern. Southern reedbuck have declined within large parts of their former range due to human settlement and depredations. They still persist along dambos within the southern catchment of the Middle Zambezi, but have declined in W Zimbabwe apparently due to increasing aridity. The large population of C Mozambique appears Near Threatened in Gorongosa and is Endangered in Zambezi Delta (Marromeu floodplain) based on a catastrophic decline since the 1970s (Cumming *et al.* 1994).

Northern Reedbuck, *Redunca occidentalis* Rothschild, 1907

Taxonomy and Distribution

Widely distributed through Gabon, N Angola, DRC, Zambia, Tanzania, and possibly N Mozambique and N Malawi. The taxonomic treatment by Ansell (1971) is provisional and it is uncertain where the two taxa (*arundinum* and *occidentalis*) actually occur in the Zambezi Basin, particularly in the southern regions. In all respects, *Redunca arundinum* (*sensu lato*) is an antelope associated with the southern savannas – a distributional pattern which distinguishes it from *R. redunca*, the Bohor reedbuck.

In conclusion, the available evidence suggests that two different populations of reedbuck occur within the Zambezi Basin; their exact distributions and taxonomic status await elucidation. Lydekker & Blaine (1914) differentiated between the two taxa on the greyer fur of the neck and grey tail of *occidentalis* compared with *arundinum*. It remains to be ascertained whether this character represents a geographical cline across Africa, or represents discontinuous variation. Overall status is Vulnerable. Reedbuck have declined in parts of Zambia, and especially in Malawi (Figure 3.5).

Table 3.1. Comparison of taxonomic units recognizing by lumping or splitting reduncine taxa at the population level within the genera *Kobus* and *Redunca* that occur within the Zambezi Basin. *K. ellispsiprymnus* in the central (and particularly NE) Zambezi Basin could be specifically distinct from the topotypical population of N South Africa and S Botswana. It is unclear whether the Tanzanian population of puku in the Rukwa and Kilombero valleys is *vardoni* or *senganus*.

Biological species		**Subspecies**	**Evolutionary species**
R. arundinum		R. a. arundinum	R. arundinum
		R. a. occidentalis	R. occidentalis
K. ellipsiprymnus		K. e. ellipsiprymnus	K. "ellipsiprymnus"
		K. e. crawshayi	K. crawshayi
		K. e. kondoensis	K. kondoensis
		K. e. penricei	K. penricei
K. leche		K. l. leche	K. leche (restricted to Okavango Delta)
		K. l. amboellensis	K. amboellensis
		K. l. notatus	K. notatus
			K. "leche - Busanga"
			K. "leche - Upemba"
			K. "leche - Luando"
		K. l. smithemani	K. smithemani
		K. l. robertsi	K. robertsi
		K. l. kafuensis	K. kafuensis
K. vardoni		K. v. vardoni	K. vardoni
		K. v. senganus	K. senganus
			K. "vardoni - Tanzania"
			K. "vardoni - Luando"
Relevant populations	**4**	**14**	**19+**
Total species	**4**	**4**	**19+**

WATERBUCK

Common Waterbuck, *Kobus ellipsiprymnus*

Taxonomy and Distribution

Two broad divisions within *K. ellipsiprymnus sensu lato* have been traditionally recognized by taxonomists. These are the *defassa* group (discussed below) and *ellipsiprymnus* group. The major character distinguishing the two forms is the elliptical ring of pale fur on the rump (*ellipsiprymnus*) versus a pale patch (*defassa*). Haltenorth (1963), followed by Ansell (1971), recognized eight subspecies under the vaguely defined *defassa* group.

It appears that the majority of waterbuck within the Zambezi Basin belong to the nominate *ellipsiprymnus*. These two species groups (*defassa* and *ellipsiprymnus*), formalized by Ansell (1971) for *K. ellipsiprymnus sensu lato*, have been recognized in later treatments (Meester *et al.* 1986), but the situation remains confused. Most importantly, the exact geographical and taxonomic relationship of *ellipsiprymnus* with *penricei, crawshayi* and *kondoensis* awaits elucidation. The relationship between *kondoensis* and *ellipsiprymnus* along the northeastern edge of the latter's range is equally unclear. The distribution of *kondoensis* centres on C and E Tanzania, but its southern limits (bordering *ellipsiprymnus*) and northern limits (bordering *thikae* (Matschie, 1910)) are unknown.

Status

Endangered in C Mozambique. Elsewhere, waterbuck are widely distributed within the southern and eastern portion of the Zambezi Basin where suitable habitat occurs and human impacts are not excessive. Ansell & Dowsett (1988) and East (1989a) do not state which taxon occurs in Malawi, but it is thought to be *ellipsiprymnus* (C. Dudley, pers. comm.)

Kondo Waterbuck, *Kobus kondoensis* (Matschie, 1911)

Taxonomy and Distribution

The distribution of the Kondo waterbuck is centred in S Tanzania, but the southern and northern limits to this population have yet to be established. It has been classified in the *ellipsiprymnus* group – apparently closely related to the nominate race (Ansell 1971). I draw attention to this population, because its possible occurrence within the northeastern margin of the Zambezi Basin needs to be considered. Here it would occur parapatrically, or perhaps sympatrically, with *ellipsiprymnus* and/or *crawshayi*.

Status

Indeterminate. This situation that can only be resolved by a thorough systematic study of this population and its allies. The population of waterbuck extending west of Lake Tanganyika to Lake Mweru could represent this *K. kondoensis* (Figure 3.2).

Crawshay's Waterbuck, *Kobus crawshayi* P. L. Sclater, 1894

Taxonomy and Distribution

Typically classified as *K. defassa crawshayi*, the distribution of Crawshay's waterbuck is centred on the southern Congo Basin west of the Muchinga Escarpment. It also has a scattered distribution across south eastern Tanzania, where its relationship with *kondoensis* is uncertain. The Muchinga Escarpment forms a significant southwestern boundary to its distribution. In a localized area along the Lusemfwa River, *crawshayi* occurs sympatrically with *ellipsiprymnus*, and hybridization has been recorded (Ansell 1978). Ansell (1982) also describes hybrids of these waterbucks near Ngoma in Kafue National Park, but no progeny appeared to survive.

In Zambia, Crawshay's waterbuck has often been called the Defassa waterbuck, *K. defassa* (for example, Hanks *et al.* 1969, De Vos & Dowsett 1966). This is strictly speaking incorrect as true Defassa waterbuck only occur in S and C Ethiopia (Ansell 1971).

Status

Vulnerable. Endangered locally within its formerly wide range. Its exact status requires elucidation of the northern extent of its distribution. Populations have been established on private game ranches in S Zambia (A. Middleton, *pers. comm*. 1990). Griffin & Grobler (1991) record the occurrence of a few individuals, which they designate *K. e. crawshayi*, in the Zambezi area of the Caprivi between 1983-1987. These are perhaps better allocated to *K. penricei*.

Penrice's Waterbuck, *Kobus penricei* Rothschild, 1895

Taxonomy and Distribution

The distribution of Penrice's waterbuck is centred in S and C Angola in the drainage of the Okavango, Upper Cunene and Kwando rivers, and the population extends marginally into the Caprivi. The type specimen was collected "from Bongo, Kuvali River, 100 miles (approx.) S.E. of Benguella" (Shortridge 1934: 528). This distribution was noted by Shortridge (1934) who, citing D.G. Lancaster (*in litt.*), mapped the range of *penricei* eastwards along the Chobe River in Angola to Shesheke in SW Zambia. In this context, *crawshayi, penricei* and *ellipsiprymnus* exhibit a parapatric distributional pattern across the region of E Caprivi and the Chobe-Zambezi confluence, a situation not followed by Ansell (1978). It remains to be established whether historical records of waterbuck along the Upper Zambezi (Ansell 1978) are referable to *penricei* or *ellipsiprymnus*.

This uncertainty is reflected in recent reviews of southern African mammals (Smithers 1983, Skinner & Smithers 1991) which do not cite the occurrence of *K. penricei* in southern Africa (the W Caprivi) and only recognize *K. ellipsiprymnus*. Nevertheless, the authoritative *Classification of Southern African Mammals* (Meester *et al.* 1986) recognizes both *ellipsiprymnus* and *penricei* as occurring in southern Africa. Here, *penricei* is listed provisionally, based on the occurrence of vagrant individuals in the Caprivi from Angola. In a final word on its status, Meester *et al.* (1986) quote W.F.H. Ansell (*in litt.*) that *ellipsiprymnus* and *defassa* (including *penricei*) form parts of a superspecies.

As with the other populations of waterbuck, the status of *penricei* is difficult to ascertain, especially with respect to *crawshayi*. Lydekker & Blaine (1914) distinguished between the darker- furred *penricei* and lighter-furred *crawshayi*. It is perhaps pertinent to note that Letcher (1910) distinguishes two varieties of "*defassa*" waterbuck – a paler-furred population south of Lake Mweru and west of the Muchinga Escarpment "in eastern Northern Rhodesia", and a darker-furred variety he only encountered and shot in the western part of the country.

Although Ansell (1971) lists *penricei* as also occurring in the southwestern DRC and S Gabon, it is unlikely that this vast area is inhabited by only a single waterbuck taxon. As with the other described populations occurring within the basin, similar taxonomic problems apply to *penricei*, a problem that can only be resolved by a thorough systematic review.

Status

Vulnerable and likely Endangered in Angola. Its exact status requires elucidation of the overall distribution of *K. penricei*, especially along its northern and eastern margins. The population of waterbuck has declined on the Kwando floodplain in Namibia. No individuals were recorded in the Kavango, Linyanti or Zambezi areas, but reasons for this decline are unknown. Some individuals, attributable to either *crawshayi* or *penricei* were recorded from the Zambezi area of Namibia (E Caprivi) between 1983 and 1987, but have not been resighted (Griffin & Grobler 1991).

LECHWE

Black Lechwe, *Kobus smithemani* (Lydekker, 1900)

Taxonomy and Distribution

The taxonomic distinctiveness of the smaller, darker coloured lechwe in N Zambia was recognized early in the 20th century, although queried by Barclay (1933). Male black lechwe had long been sought after as trophies (Lyell 1913), so this antelope was unquestionably recognized as distinct. Ansell (1964) recognized this, which had previously been unquestioned by conservation authorities. This taxonomic distinctiveness, exhibited in darker colouration and shorter horns of *smithemani*, was conclusively demonstrated by Ansell & Banfield (1980). Black lechwe formerly occurred along the northern shores of Lake Bangweulu, and also in the upper reaches of the Chambeshi River (Ansell 1978), but these populations were extirpated in the early part of this century.

Kobus smithemani only occurs along the southern and eastern margins of Lake Bangweulu, where the population migrates seasonally as water levels fluctuate. The core area used by black lechwe focuses on Chikuni Island, which only becomes isolated during high water levels (Grimsdell & Bell 1975).

Status

Vulnerable. The numbers of *K. smithemani* have recovered from a radical decline through the 1950s. The majority of this population is concentrated in the southern Bangweulu floodplain, and the localized extent of this habitat means that the population is at risk of disease (such as anthrax and rinderpest) and political unrest. A recent visit to the Bangweulu Flats in October 1999 revealed large herds in the vicinity of Chikuni Island and its surrounds. Black lechwe herds were encountered over 10 km west and 5 km east of Chikuni Island. Subsistence poaching continues as shown by the abundance of skulls a few months old on the floodplain. The population of *K. smithemani* in the western reaches of the Bangweulu Flats is exposed to commercial poachers who exploit improved access from the tarred Mansa-Serenji road (R. Nefdt, *pers. comm.* 1999).

Kafue Lechwe, *Kobus kafuensis* Haltenorth, 1963

Taxonomy and Distribution

The population of lechwes confined to the Kafue Flats of S Zambia had flippantly been described as "red lechwe" into the 1960s. The Kafue lechwe was only described as taxonomically distinct in 1963, although this had previously been suspected and even tacitly acknowledged (see Ansell 1964). *K. kafuensis* is larger than other lechwe, with larger horns (Ansell 1964). The morphology of the inguinal glands also differ from other lechwe (Ansell 1960b). *K. grandicornis*, Ansell 1964 is a synonym of *kafuensis*.

Status

Endangered. Although, the numbers of Kafue lechwe have recovered from a radical decline through the 1950s, they have not recovered to former densities or range. The majority of this population occurs in the Lochinvar National Park (with a smaller population in Blue Lagoon National Park), but is dependent on resources outside of the protected area on commercial farms and densely settled areas (East 1989a). The leks, essential for breeding, are remarkably localized in their number and location – only five existed between 1990 and 1991 within the entire range of this species on the south bank of the Kafue Flats. Despite intensive surveys, no other leks were located (Nefdt 1996). The localized extent of this habitat means that the population is at risk of disease (perhaps anthrax and rinderpest) and human depredations. A recent visit to Lochinvar in October 1999, and discussions with resident biologists and safari operators in Zambia, revealed that commercial poaching of *K. kafuensis* is rampant, especially in Blue Lagoon National Park. This situation appears to be severe and requires drastic action if the species is not to decline to extinction.

Red Lechwe, *Kobus leche* (Gray, 1850)

Taxonomy and Distribution

Based on the entrenched taxonomic classification, reduncine antelopes affiliated to the nominate race of the red lechwe are believed to exhibit an extensive, albeit scattered, distribution across the modern Zambezi Basin, with outliers in SE and C Angola, and southern Shaba province of the DRC (Ansell 1971, East 1989a, 1989b, Shortridge 1934). Red lechwe also occurred in the southern DRC in the Upemba National Park (Ansell & Banfield 1980, Schouteden 1947). An important population of lechwe occurs in S Angola, centred along the Kavango (Okavango) River and extending into the western Caprivi: the name *amboellensis* (Sokolowsky 1903) is available, with the type locality in S Angola at approximately 16°20'E and 19°30'E (Shortridge 1934). The eastern Caprivi (Linyanti) population was described as *notatus* (Matschie, 1912) and would appear to extend into SE Angola along the Luiana and Cuando rivers. The specimens noted by Ansell (1978) along the Angola-Zambian border in SW Zambia are probably from this population.

It is currently impossible to elucidate the precise taxonomic and distributional status of this complex of populations of "red" lechwes, not least because they have not been adequately studied and several appear to be extinct. Few museum specimens appear to be available. Currently allocated to *K. l. leche*, the taxonomic status of the Namibian, Angolan and DRC populations require elucidation.

Barclay (1933) concluded that no subspecific divisions were warranted in *K. leche*, but his conclusions were weakened by reliance on patterns and colour of pelage. A facile attempt at a taxonomic review by Howard & Sidorowicz (1976) concluded that all lechwe formed one species, and only two subspecies were valid. The mistakes, weaknesses and overall failure of their analysis was subsequently demonstrated, not least in being based on a false sample of *K. leche* (Ansell & Banfield 1980). The latter study focussed on the differences between *smithemani*, *robertsi* and *kafuensis* and demonstrated that *smithemani* and *leche* are the most similar in skull proportions and size, with *kafuensis* the most distinct. Given the recent diversification of lechwes (evident in *kafuensis, robertsi* and *smithemani*), it is likely that *K. l. leche* is actually a polyphyletic taxon. Radical declines in the historical range of unrecognized taxa (to extinction in *K. robertsi*), indicates that special attention should be paid to the actual taxonomic and conservation status of the plethora of populations currently attributed to *Kobus leche* (Figure 3.3).

Williamson (1994) summarized a detailed study of the lechwe in the Linyanti area of Botswana focusing on territorial and reproductive behaviour. His data demonstrated significant differences between the reproductive behaviour of this Linyanti population of "*leche*" and *kafuensis* in the timing of breeding, and other significant behavioural differences. The Linyanti lechwe are sedentary and occur at a lower density than *kafuensis*. They also defend territories of a larger size continuously through the year, and breeding adults in Linyanti differ markedly in size and colouration from *kafuensis* (Williamson 1994).

Status

Locally Endangered. Any attempt at an assessment of the status of "red lechwe" is handicapped by an inadequate taxonomy. Child (1975) records the decline of *K. leche* in the E Caprivi, which was especially noticeable on the Chobe floodplain. Here a minimum of 2500 individuals were counted in 1962 but had declined over eight years to 5% of this. Other populations of "red lechwe" are thriving (East 1989a). These include the nominate population (definitely *K. leche*) of the Okavango Delta and Caprivi, assuming these form a contiguous population. The population (possibly *K. amboellensis*) in Namibia (W Caprivi) along the Okavango River had increased from 1400 individuals in 1985 to 2000 in 1990 (Griffin & Grobler 1991). As with all lechwe, the formerly extensive range of the "red lechwe" has experienced a major shrinkage, especially within Angola and Zambia. They were formerly widely distributed across the Upper Zambezi in suitable habitat. A huge reduction in numbers and range has occurred within the Barotse floodplain, with few remnant populations persisting (Ansell 1978). The status of "red lechwe" in Angola and southern DRC requires urgent study – these are most likely Critically Endangered. Unequivocal understanding of the conservation status of the "red lechwe" is contingent on a thorough systematic review of all extinct and extant populations across their entire historical range.

Roberts' Lechwe, *Kobus robertsi* Rothschild, 1907

Taxonomy and Distribution

Only acknowledged as distinct in the late 1970s, this taxon is represented by only one population with a localized distribution in N Zambia. *Kobus robertsi* originally occurred within the Pambashye Swamps on the Luongo-Kalungwishi drainage north of Lake Bangweulu (Ansell 1978), and is certainly the most poorly known of the Reduncini, if not of all African bovids. Very few scientific specimens are known. Lydekker & Blaine (1914) listed only two specimens in the British Museum (Natural History), stating the type to be in the Rothschild Museum, Tring, and accepted *robertsi* as valid:

> "As this lechwe occurs in company with the true lechwe, it must be regarded - if anything more than a melanistic phase - as a species rather than a race." (Lydekker & Blaine 1914: 249).

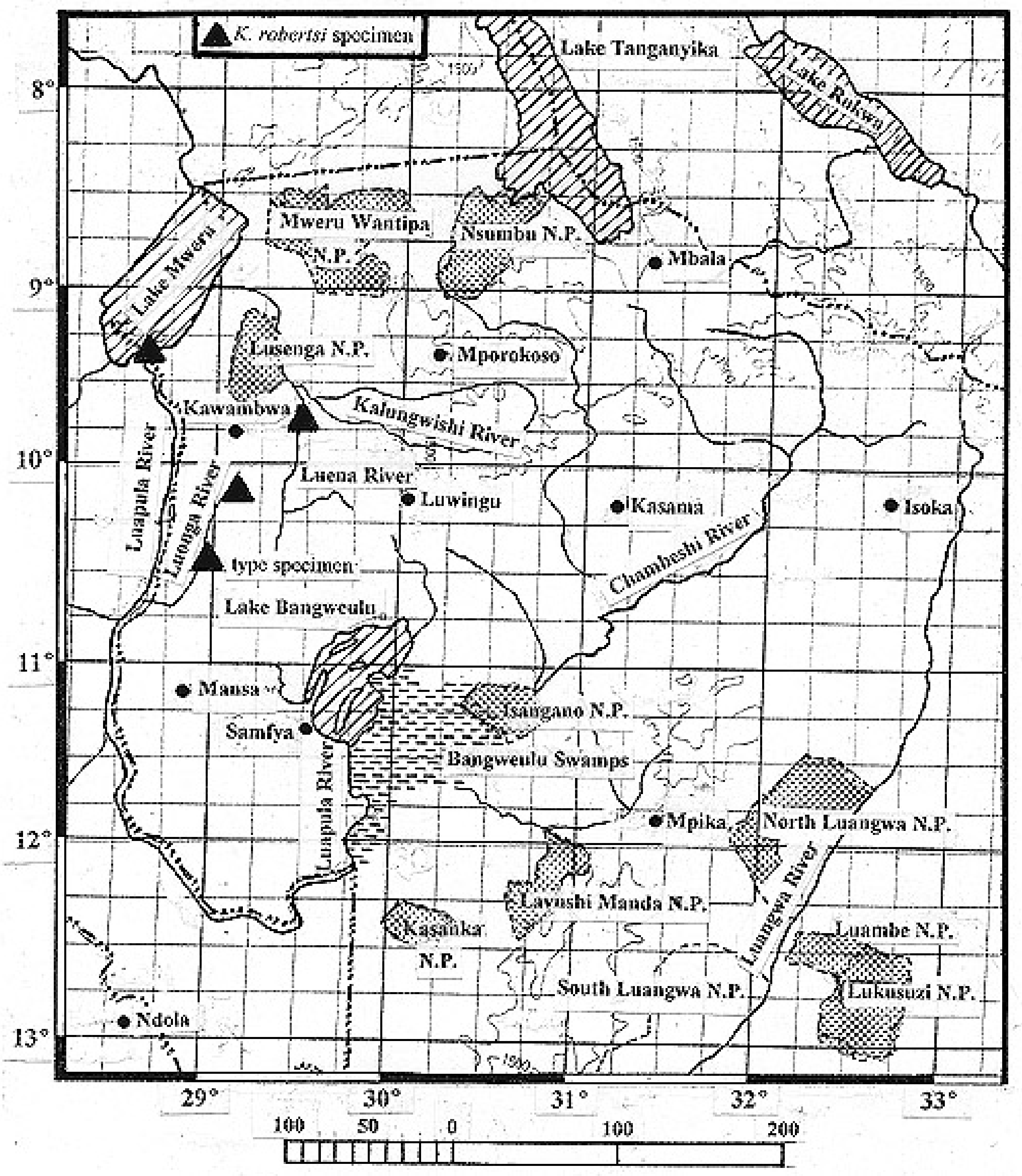
The taxon was described on the basis of only two specimens (Rothschild 1907), which were subsequently lost (Ansell 1974). Ansell (1974) allocated BM 13.11.27.1 as the neotype of *Kobus robertsi*. This was collected on the Luongo River (10°35'S; 28°59' E) on 7 October 1913. Two other specimens are known from the Luongo River (10°10'S; 29°05'E) and the Luena River (9°45'S; 29°25'E) south of its confluence with the Kalungwishi (Figure 3.6).

The type locality was restricted to the Luongo River (10°35'S; 28°59'E) by Ansell (1974). Two specimens (previously reported by Ansell 1974 as of indeterminate status) were recently reexamined in the mammal collection, Natural History Museum, Bulawayo (out of a total of 187 specimens of *K. leche sensu lato*); both specimens are in a reasonable condition. Their cranial measurements agree with that of the neotype of *robertsi* published by Ansell & Banfield (1980), and shown to be distinct from all other lechwe. These two specimens consist of a single skull (NMZB 2753 %), and skin and skull (NMZB 2751 &); both were collected from Chisenga Island (9°22'S; 28°37'E; Figure 3.6) in 1947. Situated in the south of Lake Mweru, this is north of the above mentioned localities – some 150 km northwest of the type locality of *robertsi* and the Luongo and Luena rivers (Figures 3.3 and 3.6). In total, it appears that only five specimens of *K. robertsi* are known.

Status

Extinct. Should any individuals persist they are Critically Endangered. Ansell (1974, 1978) and Ansell & Banfield (1980), followed by East (1989a), inferred *K. robertsi* to be extinct in the Pambashye Swamps and on Chisenga Island. No recent published investigation is known that has attempted to investigate the status of lechwe in northern Zambia, aside from considerable attention paid to *K. smithemani*. The relationships between collecting localities and protected areas in N

Figure 3.6. Detailed distribution of *Kobus robertsi* in northern Zambia (data from Ansell 1974, 1978, and reexamination of two specimens in the Natural History Museum of Zimbabwe) in relation to the network of protected areas. The type locality is shown.



Zambia is depicted in Figure 3.6. Virtually nothing is known about the ecology, behaviour and general biology of the Luena lechwe, aside from what can be discerned from a paucity of museum specimens and anecdotal reference in the form of very few publications. Prior to Ansell & Banfield (1980), most authorities had concluded that *robertsi* was *incertae sedis*, and glossed over its existence.

PUKU

Puku, *Kobus vardoni* (Livingstone, 1857)

Taxonomy and Distribution

Puku (*K. vardoni sensu lato*) are restricted to a limited area of the southern savanna zone, an area within the catchment of the Upper Zambezi and Luapula rivers in Zambia. The taxonomic status of the allopatric populations of pukus in Rukwa and Kilombero, S Tanzania (Rodgers 1984) and C Angola (East 1989a) is unknown. Ansell (1971) recognized two subspecies, whose distributions are separated by the Muchinga Escarpment:

> "*K. v. vardoni* (Livingstone, 1857) occurs in southern Congo basin, Angola, north eastern Botswana and Caprivi and western Zambia. It was originally described from Libonda, Barotseland by David Livingstone - where puku no longer occur."

This population also occurred eastwards along the Upper Zambezi River to the Victoria Falls (Ansell 1971, Selous 1908; Figure 3.4).

Ansell (1971) suggested that *K. vardoni* and *K. senganus* comprise a superspecies together with the Ugandan Kob, *K. kob*. Other authorities have considered the former populations to be subspecies of *K. kob*. These antelopes are morphologically uniform with similar habitat requirements, which suggests their divergence was recent (Ansell 1971). Important differences occur in the morphology of the inguinal and pedal glands between kobs and puku (Ansell 1960b).

Status

Endangered in parts of its range; elsewhere Vulnerable. Ansell (1978) emphasized that puku had declined significantly since the early 20th century. *K. vardoni* has declined significantly in NE Botswana over the past 100 years. Selous (1881) recorded the species as numerous on the Pookoo Flats, where herds of 50 were common. Puku occurred for approximately 112 km along the south bank of the Chobe upstream of the Chobe-Zambezi confluence. They also occurred at the Victoria Falls on the south bank of the Zambezi in 1874, where one was shot by Selous's colleague J. L. Garden (Dollman 1921, Selous 1908), but these were probably vagrants. More recently, Child (1968) estimated that less than 100 individuals occurred between Kasane and Simwanza along the Chobe River. Smithers (1971) reiterated that a radical reduction had occurred at the southwestern edge of their range, and this was first recorded by F.C. Selous (Dollman 1921). Ansell (1978) also noted that *K. vardoni* had undergone a significant reduction within its former range across western and northern Zambia. No information appears to be available on the Angolan populations, only on their existence (East 1989a, Machado 1969). Under adequate protection, puku populations recover rapidly. This has occurred over the past decade in Kasanka National Park in NE Zambia (Cotterill, *pers. obs*. 1999). Populations of puku introduced on to game ranches in S Zambia and into the Middle Zambezi Valley (in Zambia in the 1990s) are increasing (I. Bruce-Miller, *pers. comm*. 1999)

Senga Puku, *Kobus senganus* Sclater &Thomas, 1897

Taxonomy and Distribution

Kobus senganus occurs widely in the Luangwa Valley and eastwards into parts of Malawi (where its range has undergone significant reduction), and the Rukwa and Kilombero valleys of Tanzania (Rodgers 1984). There were recently two isolated records from the Middle Zambezi Valley in Zimbabwe, which are referable to *K. senganus*. A sighting of an adult female was recorded by Dunham & Tsindi (1984) from the Mana Pools floodplain near the Sapi-Zambezi Confluence (15°40'S; 29°35'E). Another individual (NMZB 67049 &) was collected by the Department of National Parks and Wildlife Management of Zimbabwe near Chirundu (16°02'S; 28°51'E) on 13 August 1984.

Status

Locally Endangered. The population in Zambia's Luangwa Valley appears healthy. Ansell and Dowsett (1988) concluded their status within Malawi to be precarious, with populations still persisting in the Kasungu National Park. Extirpated from large areas, but some have been reintroduced (Ansell & Dowsett 1988). Lyell (1913) emphasized that puku only occurred in C Malawi in the catchment of the Bua River. Ansell & Dowsett (1988) identified other localities north of here (Figure 3.4). The individuals recorded from the Zambezi Valley in Zimbabwe appear to be vagrants, and their persistence contingent on the establishment of a viable population – there are no previous records of the occurrence of puku in the area.

3.6 WHAT ARE THE SPECIES OF REDUNCINE ANTELOPES?

3.6.1 Defining the problem

The above overview demonstrates that the taxonomy of the Reduncini is complicated by controversies over the taxonomic status of most taxa, their unambiguous identity, and precise distributions. The current taxonomy is obsolete in its dependence on vague classifications of morphospecies within which a plethora of subspecies are subsumed. This has seriously influenced studies of reduncines and applications of biological knowledge. For example, Hanks *et al.* (1969) argued that individual waterbucks referable to both *crawshayi* and *ellipsiprymnus* occurred together in the Kafue National Park. In another example, Howard & Sidorowicz (1976) concluded that *Kobus leche* was a monotypic species with only two valid subspecies, with *kafuensis* merely a form of *K. l. leche*. More recent authorities such as Kingdon (1982, 1997), avoided major problems in reduncine taxonomy, simply by not mentioning the existence of controversial subspecies, notably in *K. ellipsiprymnus*. This is surprising because Kingdon devotes deserving attention elsewhere to the many cryptic species of primates and other mammals. A serious attempt to resolve this problem needs to briefly consider the history of mammalian taxonomy and how the entrenched taxonomy of reduncine antelopes was constructed. This provides a setting from which to understand patterns of diversification of Zambezian Reduncini more objectively.

Prior to the Neo-Darwinian Synthesis in evolutionary biology (Mayr & Provine 1980), typological perspectives often dominated taxonomy and were the *modus operandi* in mammalian taxonomy (as in many biological subdisciplines) before the biological species concept became widely adopted (Corbet 1997). Cognisance of this historical situation is important. The majority of vertebrates described and classified up until the Second World War were based on remarkably little material, and the reduncine antelopes were no exception. Rothschild (1907), for example, described *K. robertsi* as a specific taxon distinct from *Kobus leche* on the basis of only two specimens with scant comparison with other populations. The situation was exacerbated by reliance on pelage characters which vary considerably, even within localized populations.

The principal characters employed to describe species and subspecies of reduncine antelopes were pelage patterns and colouration. These formed the criteria by which taxonomists (including Lyddeker, Matschie, Rothschild and Schwarz) described numerous subspecies and species of waterbucks, reedbucks, kobs, and lechwes. The study by Ansell & Banfield (1980) is an exception in its use of cranial measurements, which justified subspecific divisions of lechwe populations subsumed under *K. leche*. With very few exceptions, all taxa of extant reduncines were described by taxonomists working before the Neo-Darwinian Synthesis had hardened. This watershed in biology more or less coincided with the Second World War, and particularly with the publication of a seminal book "*Systematics and the Origin of Species*" in 1942 by the German ornithologist Ernst Mayr, then at the American Museum of Natural History in New York (Mayr 1942). Today acknowledged as the eminent evolutionary biologist of the 20th century, Mayr provided abundant evidence that new species evolved as a result of divergence of parent populations. The key lesson of this review was that “population thinking” is essential to carefully quantify and evaluate the variation within populations in order to identify taxonomic boundaries (O’Hara 1997). Influence of population thinking on taxonomic mammalogy was apparent by the early 1950s (for example, Ellerman *et al*. 1953), but considerable research remained to be done to cope with the challenges of elucidating mammalian diversity in Africa, and indeed all biodiversity. This challenge remains, and African bovids, exemplified by the Reduncini, are not exempt. Ansell (1971) tried to resolve the taxonomy of the Reduncini (and extant African Bovidae in its entirety) by applying Mayr’s methods and philosophy of microtaxonomy, relying on the biological species concept (BSC) and, in certain cases, its derivative, the superspecies. The superspecies concept applied to waterbuck and puku to try and surmount complex taxonomic problems was not successful.

Resolution of such taxonomic problems requires objective identification of the real evolutionary products that comprise the Reduncini. This must focus on the genetically divergent populations of these semi-aquatic antelopes and further reconstruct the patterns of their diversification in space and time. The taxonomic overview given in the previous section has separated the reduncine antelopes into the smallest divisible units recognizable on the basis of morphospecies, originally described as species and subspecies. Its resolution hinges on the thoroughness with which reduncines have been scrutinized by mammalian taxonomists, and what future, more refined, analyses will reveal of other real evolutionary products in the Reduncini, especially its more cryptic taxa. My treatment obviously tends toward a splitting of taxa, as opposed to the converse treatment of extreme lumping (Table 3.1).

3.6.2 **What is a species?**

Further elucidation of reduncine taxonomy requires attention to the ontology of species, because the solution to the species problem in biology and conservation lies largely within the domain of the philosophy of science. The ontology of the entity "species" has to do with what a species actually is in terms of biological theory. Considerable controversy surrounds the species concept, and is probably unmatched by any other controversy in biology. An unambiguous species definition is very hard (if not impossible) to obtain – quite possibly one of the toughest tasks in contemporary evolutionary biology. This controversy is grounded in different perspectives on how to recognize and measure biodiversity. One approach, perhaps idealistic, has been to strive for a universal species concept, applicable to all organisms, bacteria, fungi, animals and plants; irrespective of whether they reproduce sexually or asexually. Hull (1988) has pointed out that at least two thirds of populations in the entire biosphere comprise asexually reproducing organisms, and this has been so through the geological history of life since its inception. For this reason alone (a primary dichotomy between how organisms make more organisms) a universal species concept is very difficult to obtain. This endorses a pluralistic approach to species concepts, with at least one for plants, another for arthropods, yet another for vertebrates, and more for microbes. This dichotomy between sexual and asexual reproduction need concern us no further, as all mammals reproduce sexually. We can progress to review applications of the BSC to the Reduncini.

I now devote some attention to the characterization of reduncine species. This must begin with some consensus as to what it is about species we recognize in distinguishing between diverse reduncine populations. As stated above, the impetus for attention to what species are actually lies in an oft-quoted adage that "species are the currency of conservation". Resolution of the species problem is critical to any objective assessment of organismal biodiversity and its sound study and management. The mandate for objectivity does not make this a simple exercise. The place to start is to establish deficiencies in the existing taxonomy, and then build on these through two stages to resolve the problem. I begin with an examination of the biological species concept as applied to the Reduncini and other vertebrates.

3.6.3 **The biological species concept as applied to Reduncini: superspecies or subspecies?**

The established taxonomy of the Reduncini (Ansell 1971, followed by Meester *et al*. 1986 and Grubb 1993) rests on the biological species concept (BSC). The first step before attempting an improvement of reduncine taxonomy (with a focus on the Zambezi Basin) is to review the details of how science has tried to characterize and classify populations of these antelopes. Each of the several species recognized clearly encompasses different, but frustratingly similar, populations. The latter were characterized as subspecies, or allospecies – parts of superspecies. This modification of the BSC recognized the superspecies as:

> "...consists of a monophyletic group of entirely or essentially allopatric species that are morphologically too different to be included in a single species. The principal feature of the superspecies is that geographically it presents essentially the picture of a polytypic species, but that the allopatric populations are so different morphologically or otherwise that reproductive isolation between them can be assumed." (Mayr, 1963: 499)

The superspecies concept has been widely applied to Afrotropical birds (Hall & Moreau 1970, Snow 1978 for numerous examples). Grubb (1978) inferred that a large percentage of extant Afrotropical mammals are superspecies (Table 3.2). Application of the superspecies solution to reduncine antelopes in the Zambezi Basin recognizes three superspecies comprising a total of at least twelve allospecies. These superspecies are *K. leche, K. ellipsiprymnus* and *K. kob*. This is tentative as a thorough review of the 12 populations traditionally recognized as subspecies might not elevate all to allospecies rank according to criteria of the BSC. Furthermore, following the terminology of Haffer (1986), allopatric members of a superspecies (for example, *K. leche*) are termed allospecies, while parapatric populations (*K. crawshayi* and *K. ellipsiprymnus*) are termed paraspecies (Figure 3.2).

Table 3.2. Tabulation of superspecies of African mammals as a proportion of total diversity (after Grubb 1978).

Taxa	No. species	No. superspecies	No. (and proportion) of species that are allospecies	Species/superspecies ratio
Carnivores	70-76	59	24-33(0.34-0.43)	1.2-1.3
Artiodactyls	85-96	64	36-52(0.42-0.52)	1.3-1.5
All ungulates	95-112	72	39-63(0.41-0.56)	1.4-1.7
Primates	45-69	30	25-49(0.56-0.71)	1.5-2.3
Squirrels	37	26	17(0.46)	1.3

While numerous cases of recent evolutionary divergence in African antelopes have traditionally been viewed as representing subspecific differences (and/or superspecies, Grubb 1978), recent evidence suggests that this is a superficial interpretation of the divergence that actually has occurred in these clades of recently-speciated antelope populations. Previously unsuspected divergences in some Afrotropical bovids have recently been revealed by analysis of molecular characters – in this case mitochondrial DNA of certain antelopes in East Africa. Examples include two populations of blue wildebeest, *Connochaetes* "*taurinus*" separated by the Rift Valley in East Africa. Unprecedented genetic divergence was also discovered in waterbucks, *K.* "*ellipsiprymnus*" and impalas, *Aepyceros* "*melampus*" in the same region (Arctander *et al.* 1996). It appears that future studies are likely to reveal hitherto unsuspected genetic divergence in such apparently "good" species. These developments prescribe unprecedented revision of these clades of bovids as molecular characters are incorporated into systematic revisions.

Although the biological species concept became a bastion in taxonomic zoology, its ubiquity has been widely challenged over the past two decades. The concept was originally developed for sexually-reproducing vertebrates, especially birds. The BSC has been modified and stretched in attempts to recognize species in other phyla, including invertebrates and plants, but it has encountered serious problems.

The problem with allospecies versus paraspecies or subspecies to populations, such as those of reduncines, is in the subjectivity of its application, such that some authorities might describe these reduncine taxa as semispecies given their allopatric distributions. A pertinent example is the treatment of *K. senganus*, *K. kob* and *K. vardoni* as either allospecies of one superspecies or merely subspecies of *K. kob* (Ansell 1971). In terms of the BSC (on which the superspecies concept has been built) these populations must be reproductively isolated to qualify as species. Reproductive isolation is not a prescriptive criterion for recognition of a species. Many divergent species (such as eland *Taurotragus oryx* and greater kudu, *Tragelaphus strepsiceros*) hybridize. Hybridization is not uncommon between different populations which are relevant products of evolutionary divergence. Furthermore, concern over hybridization is actually a side issue when it comes to evaluating species as divergent products of evolutionary processes. Reproductive isolation actually has only a partial role in the conceptualization of species as evolutionary lineages. This is a major danger in the interbreeding criterion of the BSC which fosters misleading interpretations of evolutionary lineages (Frost & Hillis 1990, Zink & McKitrick 1995).

The prescription by the BSC that species be reproductive isolates places a prerequisite on sympatry if a "good species" is to be unequivocally diagnosed. This is another weakness of the BSC. Ultimately, taxonomic status under the BSC hinges on geographical relationships, which are often dynamic and further subject to biases in surveys which tend to under-represent rarer taxa. Other weaknesses are that the BSC ignores some evolutionary significant entities, and does not rigorously define the ranges of species it recognizes (Cracraft 1997). An important argument against the BSC by Patterson (1985) defines a species as a population possessing a distinct SMRS (Specific Mate Recognition System). An SMRS (see below) is shared property of a population of interbreeding organisms and is subject to strong stabilising selection acting on individual organisms. A species defined by its SMRS is created entirely differently from the isolation mechanisms postulated by Mayr to maintain the distinctiveness of a biological species. According to Patterson, speciation is an effect of adaptations that evolve to support successful matings in sexually reproducing organisms. So, application of these philosophical criteria of evolutionary causation identifies yet another critical weakness in how the BSC is formulated, which limits the ability of the BSC to characterize biodiversity (Patterson 1985).

3.6.4 **Reduncine species distinguished by the Recognition Species Concept**

Given these deficiencies of the BSC, a possible solution is to apply the Recognition Species Concept (RSC) defined by Patterson (1985):

> "A species is that most inclusive population of individual, biparental organisms which share a common fertilization system." (Paterson 1985: 21)

This has particular merit in elucidation of sympatric species, especially cryptic or morphologically similar species. The SMRS of reduncine antelopes is evident in the horns and pelage patterns of the different populations. These include the facial and leg markings of different lechwes, and the different dorsal patterns of the waterbucks. Equally important are ritualistic behavioural repertoires associated with territory establishment and defence, and courtship, where visual cues are important. Olfactory cues specific to species are equally if not more important in the Reduncini (Kingdon 1982), but have only been investigated in *K. kafuensis* and *K. kob thomasi* – chemicals in female urine deposited in the soil of leks influence the reproductive behaviour of other females (Deustch & Nefdt 1992). The morphology of scent glands could be equally important traits of an SMRS, as Ansell (1960b) demonstrated for *kafuensis* and "*leche*", *kob* and *vardoni*.

Distinctly different traits distinguish species-specific SMRS of two reduncine populations traditionally characterized as representatives of two subspecies (Ansell 1971, 1974, Ansell & Banfield 1980) or two allospecies (Grubb 1978). These are *K. smithemani* and *K. kafuensis*, which differ in pelage colouration, horn morphology, skull morphology (Ansell 1974, Ansell & Banfield 1980) and semiochemistry (Deustch & Nefdt 1992). I hypothesize that evolution of a distinct SMRS has occurred in various species of waterbuck, kob and puku, and perhaps reedbuck. Elucidation of the SMRS is integral to applying the RSC to different populations of reedbuck and waterbuck.

A similar divergence is illustrated in the reproductive behaviours of *kafuensis* and the Linyanti population of "*leche*" (see above, Williamson, 1994). I infer these differences to represent a different SMRS in these two populations. Published studies of "*leche*" in the Okavango (Joubert 1972, Lent 1969) do not present data sufficient to compare with those of Schuster (1976, 1980) and Nefdt (1996) or Williamson (1994) for *kafuensis* and the Linyanti population of "*leche*". Nevertheless, the outline of divergences between the SMRS of certain reduncines can be summarized in Table 3.3.

Table 3.3. Comparison of some semio-chemical, behavioural and morphological traits documented for certain populations of the Reduncini of the genus *Kobus* indicative of a Specific Mate Recognition System. The emphasis is on comparison of differences with closely related species of lechwe, kob and waterbuck. Data obtained from Allen (1963), Ansell (1960b, 1964, 1974), De Vos & Dowsett (1966), Grimsdell & Bell (1975), Hanks *et al.* (1969), Kingdon (1982), Lent (1969), Leuthold (1977), Nefdt (1995, 1996), Robinette & Child (1964), Rosser (1987), Schuster (1976), Skinner & Smithers (1990), Smithers (1983), Thirgood *et al.* (1992) and Williamson (1994).

Taxon **Trait**	**smithemani**	**leche - Linyanti**	**leche - Kasempa**	**kafuensis**	**kob**	**vardoni**	**crawshayi**	**ellipsiprymnus**
Mating system	polygamous territories	aseasonal lek	?	temporary lek	seasonal lek	resource defence mating system	polygamous territories	polygamous territories
Scent	?	?	?	specific?	specific?	?	?	“turpentine” tainted fur
Pedal glands	?	?	?	?	?	vestigial	?	?
Inguinal glands	?	?	open anteriorly	open laterally	open ventrally	open anteriorly	?	?
Coloration	black pelage in adults	dark stripe on foreleg	?	foreleg stripe, patch on neck	black forelegs	rufous forelegs	pale rump patch, dark neck & flanks	pale ring on rump
Body size	smallest	intermediate	intermediate	largest	_	_	_	_
Horns	smallest	intermediate	intermediate	largest	_	_	_	_

Although the RSC appears to confer major strengths to characterize reduncine species, its major weakness is its non-historical limitations (as for the BSC). It cannot recognize the temporal dimension of species – that they are lineages. Neither the RSC nor BSC recognize that species – reduncine antelope or other – are lineages with a birth (speciation) and a death (extinction). These problems have received the attention of phylogenetic systematists since the early 1980s as part of the spread of historical perspectives through systematics, culminating in widespread adoption of cladistic philosophy and its methods in recognizing and classifying taxa. This philosophy – termed tree thinking (O’Hara 1997) – has radical implications for how we conceptualize species (Ghiselin 1997).

Speciation can be caused by many different processes driven by different determinants of disturbance and selection. An important commonality to speciation is that most species are believed to form in geographical isolation – in allopatry. An important set of processes results in vicariance – the disruption of populations’ ranges in a geographical context. In terms of the RSC, the primary change in speciation in a sexually reproducing population as in mammals) is the formation of a new SMRS. Thus a mammalian species has a birth and death, with the overall temporal pattern being the origin and extinction of its SMRS.

3.6.5 Recognizing that Reduncine species have an evolutionary dimension

Complementary to population thinking, tree thinking conceptualizes extant individuals of a species not just as populations occupying some geographical zone, but also as the living parts of a historical lineage. Cognisance of a temporal, as well as a spatial, attribute of species has generated a number of historical species concepts. A major impetus for recognizing a temporal dimension to species concepts was the widespread adoption of phylogenetic perspectives in systematics (Baum 1992). Although both developed through the 1980s, phylogenetic treatments of species have scarcely interacted with the parallel development of the Recognition Species Concept. Distinct allopatric populations are distinct lineages, and thus phylogenetic species, but may still maintain the same SMRS.

Atemporal deficiencies of the BSC and RSC can be overcome if we consider the evolutionary divergence of populations. Tree thinking recognizes a commonality to all episodes of speciation with respect to the underlying pattern. Species result when a population exhibiting continuous variation has diverged to produce two or more populations exhibiting a pattern of discontinuous variation. Thus, the patterns of horn shape and size, skull morphology and pelage colour in *K. kafuensis* and *K. smithemani* exhibit a classic example of discrete variation, although the traits used as taxonomic characters vary continuously within each population.

Mayr (1957) originally distinguished between primary and secondary concepts of species. With the notable exception of Mayden (1997), this key distinction has been ignored in the plethora of publications seeking to resolve the species problem in evolutionary biology. The only concept that qualifies as a primary species concept is the Evolutionary Species Concept (ESC) originally proposed by Simpson (1951, 1961) and developed subsequently (Mayden 1997, Wiley 1978). No matter the mechanisms underlying its formation, any species (plant, microbial or animal) is an evolutionary species. A primary property of any species – whether comprised of sexual or asexual organisms – is that it persists as a lineage through time. This property underpins the primary species concept as articulated in the Evolutionary Species Concept (Mayden 1997, Simpson 1961):

> "...an entity composed of organisms which maintains its identity from other such entities through time and over space, and which has its own independent evolutionary fate and independent tendencies." (Wiley & Mayden 1997, quoted in Mayden 1997: 395).

3.6.6 Characterization of the evolutionary species of Reduncine antelopes

The stated objective to cleave nature at its historical joints so as to identify real evolutionary entities, is to ensure that no distinct biodiversity falls through the cracks in the conceptual maps we construct of its patterns of divergence. Fissured taxonomies (exemplified by artificial treatments such as adherence to the typological belief that all lechwes are "red lechwes") are inaccurate and prevent characterization of real evolutionary products. Complete and rigorous characterization of a species needs to apply the Evolutionary Species Concept (ESC) as the primary concept of species applicable to all biodiversity. In practice, this exercise encounters a severe hurdle.

The ESC is not operational, and secondary concepts are required to recognize a species depending on whether the population is sexual or asexual, and whether it has (or does not have) fossilized representatives of its extinct parts. In philosophical terms, application of the ESC as the primary species concept, using secondary species concepts to recognize evolutionary lineages applies a combination of monism and pluralism (Mayden 1997), a strategy followed by Dimmick *et al.* (1999). A pluralistic solution uses secondary species concepts (notably recognition, RSC, and phylogenetic, PSC) to discover species. Following Baum & Donoghue (1995), a similar strategy has been employed by Soltis and Gitzendanner (1999) in characterizing botanical diversity using a historical application of the phylogenetic species concept. This approach is revolutionary, and the conservation lessons and implications are extreme (Dimminck *et al.* 1999, Soltis & Gitzendanner

1999); because it objectively elucidates the actual products and patterns of diversification. A similar conclusion is drawn by de Queiroz (1998), who emphasizes that the RSC is more fine-grained and identifies smaller-scale properties of species, whilst the PSC takes a broader-scale view of a species in considering its entire lineage.

Nevertheless, characterization of evolutionary species is difficult, especially where fossil data are scarce or non-existent (as with the Reduncini). To move beyond the deficiencies of the current reduncine taxonomy based on the biological species concept, I see the only solution is to apply both the RSC and PSC. This means that in applying a pluralistic conceptualization of species to the Reduncini and other mammals we must define a species as:

> an interbreeding population that has diverged from related species and possesses a common specific mate recognition system (SMRS). This unique lineage of sexually-reproducing organisms experiences a birth and death and exists as a genetically exclusive population.

3.6.7 **Diversification in Reduncine species using the phylogenetic species concept**

The application of a phylogenetic species concept (PSC) is not without its difficulties and controversies. The PSC has gathered major support and revolutionized perspectives of biological diversity in several groups, especially birds (Cracraft 1997, Martin 1996). Attempts to overcome deficiencies of the BSC have fuelled much of the impetus for phylogenetic and historical perspectives to define species and their properties. An example of the application of a phylogenetic species concept is a recent revision of African tree frogs (Schiotz 1999), which reveals considerable biodiversity previously unrecognized. Another is the application of a phylogenetic species concept to extant birds (Cracraft 1997) in which hitherto hidden biodiversity is revealed. The implications of this refined knowledge in conservation are extreme (Peterson & Navarro-Siguenza 1999, Soltis & Gitzendanner 1999).

It is important to realize that many versions of the PSC have been proposed (as emphasized by Baum 1992, Baum & Donoghue 1995, Mayden 1997, Soltis & Gitzendanner 1999). Their derivation and application falls into one of two philosophies of systematics - pattern cladistics or phylogenetic systematics. Their differences have important implications for how a particular PSC characterizes biodiversity. Based on pattern cladism, a widespread application of the PSC is diagnostic, as originally stated by Cracraft in 1983:

> "...the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." (Cracraft 1983: 170)

The major problem with any diagnostic PSC is its subjectivity in recognizing diagnosable groups. They fail to define genetically-exclusive populations. A population perspective is an imperative requirement of a robust species concept. This was attempted by the BSC, is a strength of the RSC, and a failure of the diagnostic PSC. Nevertheless, all these concepts fall short in either reproductive inclusiveness (diagnostic PSC) or historicity (recognizing the species as a lineage - BSC and RSC). An important and recent development in phylogenetic systematics has been to recognize and quantify the historical dimension of species, focusing on their exclusivity (Baum 1992, De Queiroz & Donoghue 1990). This would seek out genetically-exclusive populations for objective characterization (*sensu* Baum & Donoghue 1995), and recognize their existence as historical lineages by describing them as phylogenetic species. Baum & Donoghue (1995) emphasize the importance of genetic exclusivity in applying a phylogenetic species concept to populations. This ideally requires elucidation of gene trees using molecular characters, but exclusivity of a lineage can be established from comparisons of morphological and behavioural characters. It cannot be overemphasized that this "history-based" approach is fundamentally different from the diagnostic PSC advocated by Cracraft (1983, 1997) and pattern cladists (e.g. Nixon & Wheeler 1990). Baum & Donoghue (1995: 566) define species under a history-based PSC as ".as basal, exclusive taxa; that is, taxa containing within them no subgroups that are themselves exclusive.", such that a species is:

> "a basal group of organisms all of whose genes coalesced more recently with each other than with those of any other organisms outside the group." (Baum & Donoghue 1995: 567)

This theoretical framework of this species concept focuses on the genealogical history of populations rather than on the presence or absence of characters as applied in diagnostic PSC. Characters are used to characterize history-based phylogenetic species, but are fallible evidence for the existence of a species, rather than its defining attributes. Ideally, reconstructions of gene coalescence are needed to characterize species using this concept, but morphological characters can equally be used (Baum & Donoghue 1995).

The first step toward an objective characterization of reduncine species applied the RSC (in actual fact a secondary species concept - Mayr 1957, Mayden 1997) to the fine-scale properties of a species in a time-limited context. This focused on characterization of Specific Mate Recognition Systems (SMRS). The characters associated with these in a reduncine population are likely to be associated with genetic exclusivity of particular lineages. Nevertheless, through vicariance, evolution of a genetically exclusive population of reduncines may occur without modification of the SMRS. Characterization of evolutionary lineages in the Reduncini requires a species concept that accommodates an entity extended through time. Here, application of a historical PSC (following Baum & Donoghue 1995) that utilizes molecular and morphological characters of reduncines would characterize exclusive populations in terms of their phylogenetic relationships.

3.6.8 **Conclusions and recommendations**

(a) In any taxonomy (applying the BSC or a more biologically-appropriate species concept), the taxonomic status of the reedbucks is currently too unclear to recognize unequivocal divisions between the northern or southern reedbucks (*R. occidentalis* and *R. arundinum*, respectively). This problem is compounded by the hazy understanding of exact ranges of the two populations within the Zambezi Basin. This particular problem can only be resolved by thorough review of museum specimens. This also applies to certain waterbuck populations – *crawshayi* and *penricei* are recognized as species distinct from the "*ellipsiprymnus*" in Zimbabwe and E Zambia. The precise status of the latter population, and those elsewhere in the Zambezi Basin requires review, as does that of *kondoensis*.

(b) In this phylogenetic context the ESC (Mayden 1997), rendered operational by the historical PSC and the RSC, recognizes at least 18 extant species of Reduncini within the Zambezi Basin (Table 3.1). Application of the PSC characterizes all allopatric populations of lechwe as distinct species. Equally, *senganus* and *vardoni* are kob species separated by the Muchinga Escarpment. It is most important to emphasize that this figure is tentative – it is especially weakened by dependence on morphospecies. Characterization of the true identities of the phylogenetic species in the Reduncini requires deeper understanding of their biogeography and phylogeny. It is likely that the figure is higher if other unstudied populations within the basin and surrounding wetlands are considered. This uncertainty particularly applies to lechwe, and waterbuck, puku and reedbuck populations in E Angola. In particular, the localized populations of *K.* "*leche*" and *K.* "*vardoni*" in C Angola are singled out for urgent study.

(c) Possible divergence between the "red" lechwe in the drainage systems of the Okavango and Linyanti deserves consideration. I hypothesize that *K. amboellensis* in the Cubango (extending into W Caprivi) and *K. notatus* in the Linyanti (and higher up the Luiana and Cuando rivers) could be distinct from topotypical *K. leche* of the Okavango Delta, each evolved allopatrically within its respective drainage system. Although these populations might appear contiguous, this may not have been so in the recent geological past considering tectonic modifications.

(d) The database of characters and specimens for Reduncini available to me is too incomplete to revise the Reduncini at present. Given the scope and complexity of this problem, it has only been possible to carry out a tentative overview of the reduncine populations – as summarized above – to attempt some synthesis of the patterns of their diversity within the Zambezi Basin, and so account for its origin.

(e) Recalling the imperative to "carve nature at her historical joints", and so reveal relevant evolutionary products, the need to resolve the taxonomy of all extinct and extant Reduncini requires an exhaustive revision. This will need to include morphological, behavioural and (especially) molecular characters at a continental scale with recourse to the type material of all described taxa. Nothing short of a thorough systematic review can solve the current uncertainties and complexities. The key in such an investigation may prove to be the use of molecular characters in cladistic analyses to resolve a phylogeny, especially for parapatric and sympatric species. The sitatunga populations, extending from the Okavango-Caprivi through Barotseland and across N Zambia to Lakes Bangweulu and Mweru (with an isolated population in C Angola occurring with puku and lechwe), also deserve the scrutiny of the philosophies and practices of modern systematics.

3.7 EVOLUTION OF REDUNCINE ANTELOPES IN THE ZAMBEZI BASIN

3.7.1 **Evolutionary changes and vicariance**

Integral to an objective characterization of biodiversity is to characterize the processes that have driven speciation. Speciation is an effect – a consequence – of processes that caused populations to diversify into distinct evolutionary lineages. New species form through different mechanisms, which include vicariance, sympatric speciation (perhaps driven by sexual selection) and genetic drift within certain demes in a population. In the case of reduncine antelopes, the mechanism of speciation has most likely involved changes in the SMRS of fragmented populations caused by directional selection. The most likely explanation is that a combination of climatic change and tectonic movements caused vicariance of reduncine populations across the basin. The greatest degree of vicariance has occurred on the African peneplain where the drainage of the Upper Zambezi has shifted dramatically through the Tertiary and Quaternary. Equally importantly, natural and sexual selection operated within these populations in allopatry (and parapatry) to result in the evolution of specific SMRS in different populations.

As an agent of reduncine evolution, the impact of vicariance can be singled out. The shared genetic composition of a population would have been changed by natural selection and been sorted by environmental changes. Climate-induced changes, especially arid periods, would have shrunk a contiguous wetland (such as N Zambia and the southern portion of Shaba Province) into isolated fragments of aquatic habitat. Natural selection, within separated habitats under different environmental conditions, could have driven the evolution of species-specific adaptations for mating. Perhaps a major agent of such change would be sexual selection operating within the polygynous mating system of reduncine antelopes. A different SMRS – and thus species – could evolve as an effect of organismal reproduction in geographically isolated populations under the influence of directional selection. The overall result of vicariance was the origin of new populations – each persisted as a distinct species.

Environmental change through the late Tertiary and Quaternary has long been postulated as responsible for diversification of African vertebrates. Recent reviews of evolution in African mammals (Grubb 1978, 1982, 1983) have benefited from a far more complete biogeographical database then was available to researchers in the 1920s who first suggested that environmental changes drove diversification (e.g. Ruxton & Schwarz 1929). These more complete data have allowed recent authors to draw more comprehensive conclusions about other faunas (e.g. Carcasson 1964, Crowe & Crowe 1982, Hall & Moreau 1970, Moreau 1966, Snow 1978). Consideration of the expansions and contractions of forest, savanna and semiarid habitats across Africa, before and through the Pleistocene, has been central to all these reviews of biotic evolution in the Afrotropical realm. As discussed above, Grubb (1978) provided a thorough overview of Afrotropical mammals at a continental scale, and applied the biological species concept to distinguish superspecies. A refined analysis is still required that needs to utilize thorough, fine-grained biogeographical datasets in conjunction with molecular data to reconstruct gene trees and more robust phylogenies, using an evolutionary species concept.

3.7.2 Evolution of wetlands through the late Tertiary

These previous reviews (with partial exception of Ansell 1960a) adopted a rather coarse-grained approach at a continental scale, and have also tended to focus on forests (Grubb 1978, 1982, 1983, Robbins 1978, Kingdon 1981). The evolution and biogeography of semi-aquatic mammals possibly differs from forest-dwelling and other terrestrial populations, that have primarily been influenced by climatic changes. The vicariance of aquatic habitats in Africa with respect to mammal evolution has received comparatively little attention, and the Reduncini are exceptional in their predilection for aquatic habitats. Equalling, if not exceeding, the climatic changes in impacts, there is considerable evidence that Africa's drainage systems and basins have been altered repeatedly. This has been caused by geomorphological agencies, including tectonic activity and capture of headwaters, and is especially true of the African erosion surface across what is today Zambia, Tanzania, E Angola, Botswana, N Mozambique and southern DRC. Situated on the ancient African plateau, the hydrology of the Zambezi and associated tributaries has changed repeatedly and radically (Partridge & Maud 1987, Thomas & Shaw 1988, 1990).

The African surface is ancient when considered in a geomorphological context – the African peneplain was established early, soon after Gondwanaland had split up. Its formation began in the Mesozoic, and has been partially eroded through two Post-African events for at least 35 million years. The drainage across the continent exploited zones of crustal weakness surrounding the cratons of more ancient rocks (Partridge & Maud 1987). Slight alterations of this comparatively level surface by tectonic events has radically modified drainage patterns across the subcontinent across a range of spatial scales (Main 1992, Skelton 1994, Thomas & Shaw 1988, 1990).

Burgeoning data point to the importance of vicariance in having generated a significant portion of global biodiversity. The resultant biogeographical pattern is frequently associated with allopatric populations exhibiting little morphological divergence (Dimmick *et al.* 1999). This is true of the Reduncini and other Afrotropical mammals where numerous allopatric populations (traditionally and variously interpreted as super- or subspecies) have evolved since the Pleistocene. These biogeographic patterns deserve wider and more detailed attention and their elucidation is critical to understand the evolutionary processes which generated the region's biodiversity. The implications for conservation decisions and activities cannot be over emphasized.

3.7.3 **Evidence from other Zambezian mammal species**

The Zambezian drainage has been radically altered over the past five million years (Main 1992). Two major events can be singled out. Firstly, the connection between the Upper Zambezi and Limpopo was closed by the end of the Pliocene (5 Mya), as concluded by Thomas & Shaw (1988, 1990). Their respective fish faunas vary more than that of an equivalent comparison of the Upper Kafue, Upper Zambezi and Okavango, the fish faunas of which are very similar (Skelton 1994). This would not have influenced reduncine evolution, given recent speciation. Secondly, the capture of the Upper Zambezi, Upper Kafue and other Upper Zambezi tributaries by the Middle Zambezi, which is the more likely agency of reduncine evolution.

Notable patterns exhibited in the distributions of Reduncini within the Zambezi Basin parallel those of other large mammals. (Figure 3.7, Table 3.4). The predominant pattern is one of vicariant species distributions – this especially applies to organisms whose capabilities of dispersal were minimal during vicariant disturbances. The common consequence for such populations would have been widespread extinction with local persistence of fragmented populations. Within the Zambezi Basin, additional patterns of divergence and disjunct distributions are exemplified in several populations of closely related populations of mammals (Figure 3.8). Particularly pertinent are certain endemic mammals of the Luangwa Valley, including Thornicroft's Giraffe, *G. thornicrofti* and Cookson's Wildebeest, *C. cooksoni*. Other large herbivores, including two closely related sable antelopes (*Hippotragus niger* and *H. anselli*), exhibit a similar biogeographical pattern (Groves 1983). The distributions of the two sun squirrels, *Heliosciurus mutabilis* and *H. gambianus*, are also divided by the Muchinga Escarpment (Ansell 1978).

Also noteworthy is that a distinct population of Tsessebe, *Damaliscus lunatus* is restricted to the Kasanka Flats and Mpika area south of Lake Bangweulu (Ansell 1978, Bell and Grimsdell 1973). This population is separated by hundreds of kilometres from a southwestern population (occurring from N Botswana, through W Zambia (west of the Upper Zambezi) into E Angola). The Bangweulu population of *D. lunatus* is perhaps more closely related to *D. l. jimela* (Matschie, 1892) of East Africa (where it is commonly called the topi). I hypothesize that vicariance between the Bangweulu and west Barotse populations of *D. lunatus* followed the alteration of Upper Zambezi drainage – a portion of the original Chambeshi and other south easterly flowing rivers were captured by the Kafue and Lusemfwa, the latter being tributaries of the Middle Zambezi and Luangwa, respectively. This event followed either tectonic activity or headwater capture, or both Tsessebe exploit the ecotone between savanna and floodplain; and would have been distributed along the course of the Chambeshi-Upper Kafue to its confluence with the Zambezi. It is pertinent to record that the distinctly allopatric distribution of *Damaliscus lunatus* (*sensu lato*) across the Upper Zambezi-Kafue-Chambeshi cannot be easily discounted as the result of a historical decline.Without exception, historical evidence (Dollman 1921, Grimwood *et al.* 1958, Knowles Jordan & Ansell 1959, Letcher 1910) all emphasizes (and indeed puzzles over) the anomalous distribution of tsessebe across what can now be recognized as the Upper Zambezi, Upper Kafue and Chambeshi-Luapula axis.

Further evidence lies in the distributions of primates. A distinct biogeographical pattern can be singled out for baboons and forest guenons, with two assemblages separated across an axis extending from the Chambeshi to Shesheke and Okavango (hereafter the Chambeshi-Okavango axis). This axis follows a NE-SW trend, and in Zambia coincides with the drainage of the

Figure 3.7. Proposed evolution of the drainage systems across the Upper Zambezi Basin and its environs, and the resultant vicariance of lechwe antelopes. Hatching depicts possible zones where populations have diverged into their present allopatric distributions. Recent historical declines are not depicted. Evolutionary species of lechwes are depicted by numbers:
1 *leche* (Okavango Delta); 2 *amboellensis*; 3 *notatus*; 4 "leche – busanga"; 5 "leche – Upemba"; 6 "leche – Luando"; 7 *smithemani*; 8 *robertsi*; 9 *kafuensis*.

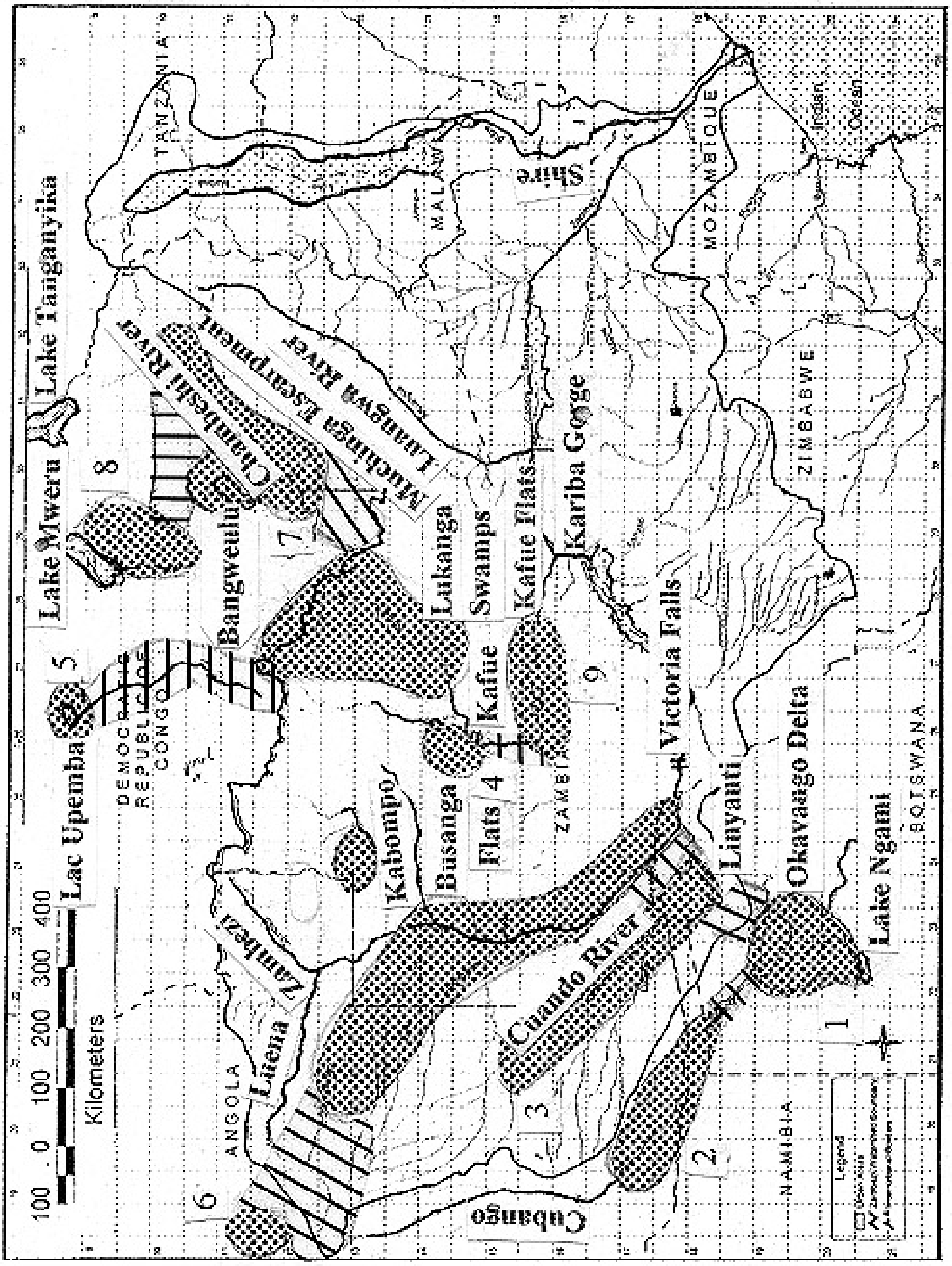


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Table 3.4. Checklists of wetland antelopes occurring in the principal wetlands of the Zambezi Basin and its environs. Although not strictly adapted to wetlands, tsessebe, giraffes and oribi are included as their biogeography correlates closely with that of reduncines (X - taxon occurs in locality; ? - occurrence uncertain; E? - occurrence uncertain, but if present then endangered).

Category	Bangweulu	Mweru	Barotse	Okavango	Chobe/ Linyanti	Kafue Flats	Lower Shire	Luangwa Valley	Zambezi Delta
Reduncines									
Redunca arundinum Southern Reedbuck	?	?	?	?	?	?	?	?	?
R. occidentalis Northern Reedbuck	X	X	X	?	?	?	?	?	?
Kobus crawshayi Crawshay's Waterbuck	X	X	X		?	X			
K. ellipsiprymnus Common Waterbuck				X	X	X	X	X	?
K. kondoensis Kondo Waterbuck	?	?						?	
K. penricei Penrice's Waterbuck				?	X				
K. kafuensis Kafue Lechwe						X			
K. leche Red Lechwe			X		X				
K. robertsi Roberts' Lechwe		X							
K. smithemani Black Lechwe	X								
K. senganus Senga Puku							E?	X	
K. vardoni Puku	I	I	I		I	I			

Category	Bangweulu	Mweru	Barotse	Okavango	Chobe/ Linyanti	Kafue Flats	Lower Shire	Luangwa Valley	Zambezi Delta
Other Species									
Giraffae thorncrofti Thorncroft's Giraffe								X	
G. angolensis Angolan Giraffe			X	X	X				
Damaliscus lunatus Tsessebe			X	X	X				
D. "*lunatus*"-bangweulu Bangweulu Tsessebe	X								
Tragelaphus spekei Sitatunga	X	X	X	X	X				

Figure 3.8. Distributions of certain species of large herbivores: wildebeest (*Connochaetes taurinus* and *C. cooksoni*), tsessebe (*Damaliscus lunatus*), giraffe (*Giraffae angolensis* and *G. thornicrofti*). Information compiled from Ansell (1978) and Ansell & Dowsett (1988). Historical declines are not distinguished.

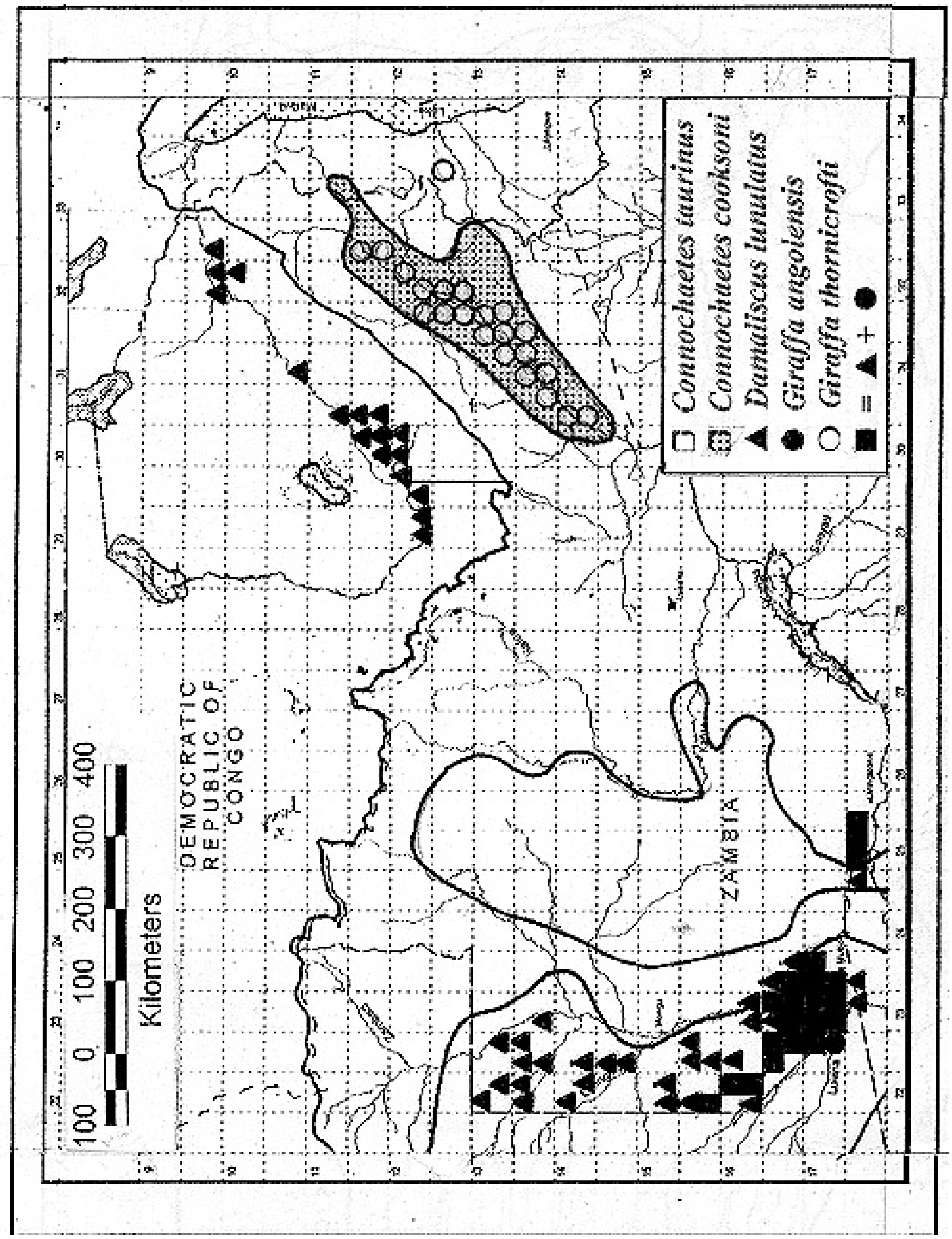
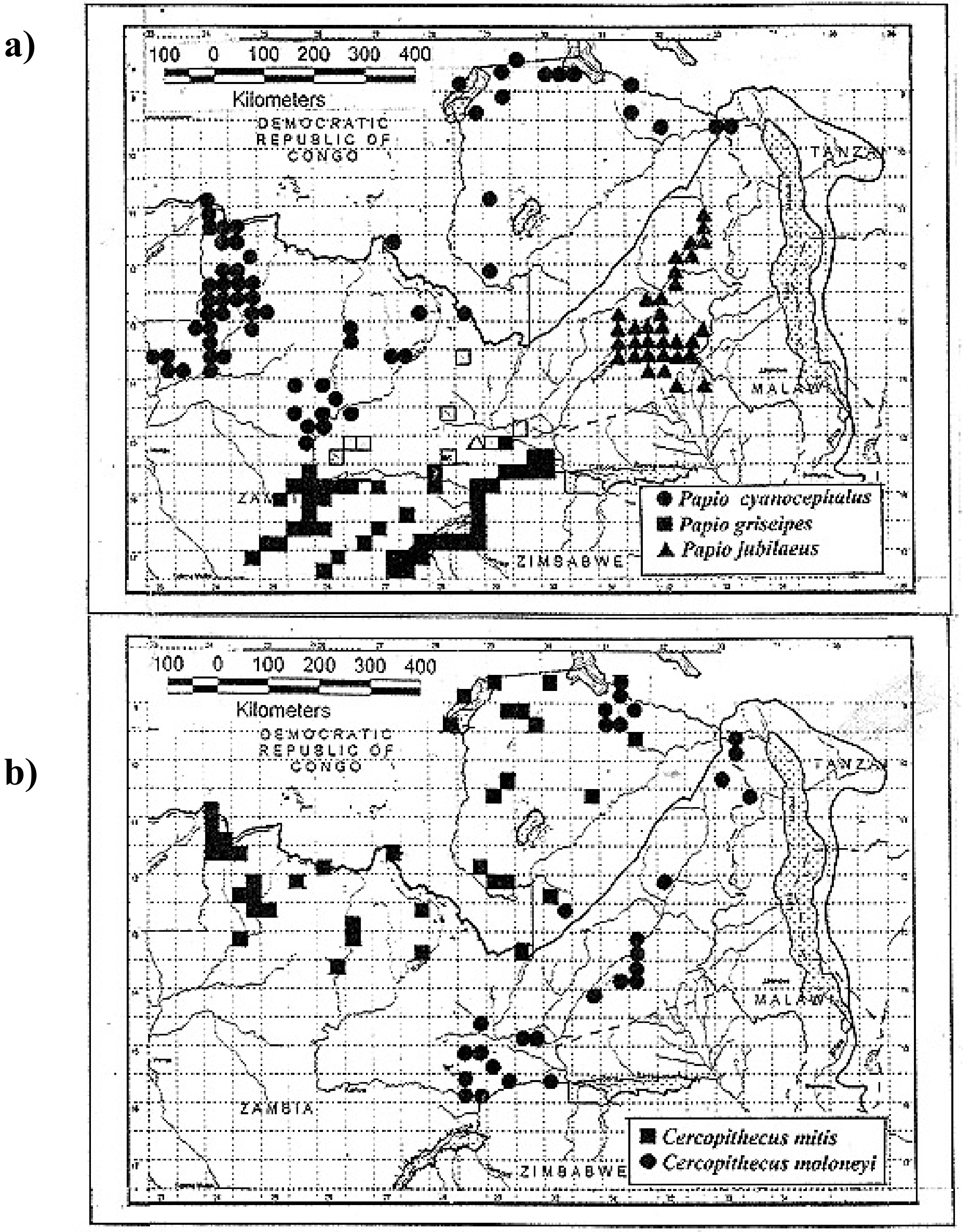


Figure 3.9. Distributions of three evolutionary species of (a) baboon (*Papio cynocephalus*, *P. griseipes* and *P. jubilaeus*) and (b) two evolutionary species of forest monkey (*Cercopithecus mitis* and *C. moloneyi*) demonstrating allopatric distributions (data from Ansell 1978). While *P. jubilaeus* only occurs east of the Muchinga Escarpment, *P. griseipes* and *C. moloneyi* are separated from related populations by the former course of the Upper Zambezi and Chambeshi drainage systems. Open symbols represent localities for which the species identity is in doubt.



Chambeshi and Upper Kafue rivers. Blue monkey, *Cercopithecus opisthostictus* Sclater, 1893 and yellow baboon, *Papio cynocephalus* (Linnaeus, 1766) occur to the north, and chacma baboon, *P. ursinus* (Kerr, 1792) and *C. moloneyi* (Sclater, 1894) are restricted to the south of this Chambeshi-Okavango axis (Figure 3.9). This relationship is also seen in the speciation pattern of *K. kafuensis* (see below, and Figure 3.3), separated from more northerly lechwe populations of the Upper Kafue (Busanga and Lukanga Swamps). Significantly, the divergence between *Papio griseipes* and *P. jubilaeus* – two allopatric populations of baboons (both occurring south of the Chambeshi-Okavango axis) – occurs along the Muchinga Escarpment (Figure 3.9a).

These major changes in Africa's mammal fauna are parallelled to a lesser extent in the divergences represented in many species of extant mammals occurring in and around the modern Zambezi Basin. The Upper Zambezi, notably the Barotse floodplain, appears to be a major geographical barrier (not only to many large mammals, but amphibians and reptiles too) between mesic and xeric species. Pertinent examples are *Connachaetes taurinus*, *Giraffae angolensis,* and *D. lunatus* (Figure 3.8), as well as *K. crawshayi* and *K. vardoni* (Figures 3.2 and 3.4). The contemporary annual flooding regime may prevent lateral dispersal, but it does not explain why dispersal did not occur during arid periods in the late Pleistocene – only tens of thousands of years ago. The existence of apparently recently-diverged taxa (exemplified by tsessebe) suggests that some dispersal has occurred and/or vicariance has been recent. The likely mechanism is that tectonic activity altered the geographical pattern of drainage across an axis extending from the Bangweulu-Chambeshi drainage system into the modern Okavango-Makgadikgadi. The Chambeshi and Upper Zambezi are hypothesized to have flowed into this inland lake – the Makgadikgadi. Several mammals with a predilection for open savanna (such as alcelaphine antelopes) and/or aquatic grasslands (reduncine antelopes) would then have exhibited a more continuous distribution.

As with reduncines, these resultant products of this diversification have been typically interpreted as superspecies (Grubb 1978). The situation is obviously ripe for a radical revision of these zoogeographical patterns using the refined concepts and methods of phylogenetic systematics. Although the pattern of speciation has been traditionally termed allopatric (or parapatric), the more appropriate term is dichopatric (following Cracraft 1984) in order to recognize that the major process of diversification for evolution of reduncines and other large mammals across the Zambezi Basin has resulted from vicariance, and not competitive exclusion.

3.7.4 **Diversification of Reduncine antelopes in the Zambezi Basin**

The divergence exhibited among extant representatives of the Reduncini strongly suggests that speciation was not simply caused by a single disturbance event, and neither were these disturbances a simple result of one agency. It appears that several species originated across a shifting mosaic of islands of wetland in a sea of predator-rich savanna. A similar pattern of allopatric speciation is exemplified by the giraffe, wildebeest and tsessebe, large herbivores of open savanna. The resultant pattern of diversity in modern reduncines is today a fragmented mosaic. In historical times, much of this biogeographic mosaic of reduncines within the Zambezi Basin has been destroyed by human depredations and impacts over the past two centuries. Preliminary scrutiny of the lechwes reveals that at least four species occur within Zambia alone, and possibly the populations of Barotseland, Busanga Flats, Caprivi and the Okavango are genetically distinct. There are also populations (designated as *K. l. leche*, Ansell 1978, Ansell & Banfield 1980) represented by specimens in the Royal Museum of Central Africa, Tervuren, Belgium from the Shaba Province of the DRC. These are mainly from the environs of Lake Upemba (Schouteden 1947). Their precise taxonomic status has yet to be established (Ansell & Banfield 1980; see species accounts above).

The marked difference between the distributional patterns of lechwe versus waterbuck in modern Zambia suggests one of two scenarios regarding diversification (Figure 3.10): (a) populations of these two groups diverged in response to two separate episodes of vicariance, or (b) the founder population(s) responded differently to the same environmental changes. Examples illustrate the possible role of these processes in the major vicariant events hypothesized:

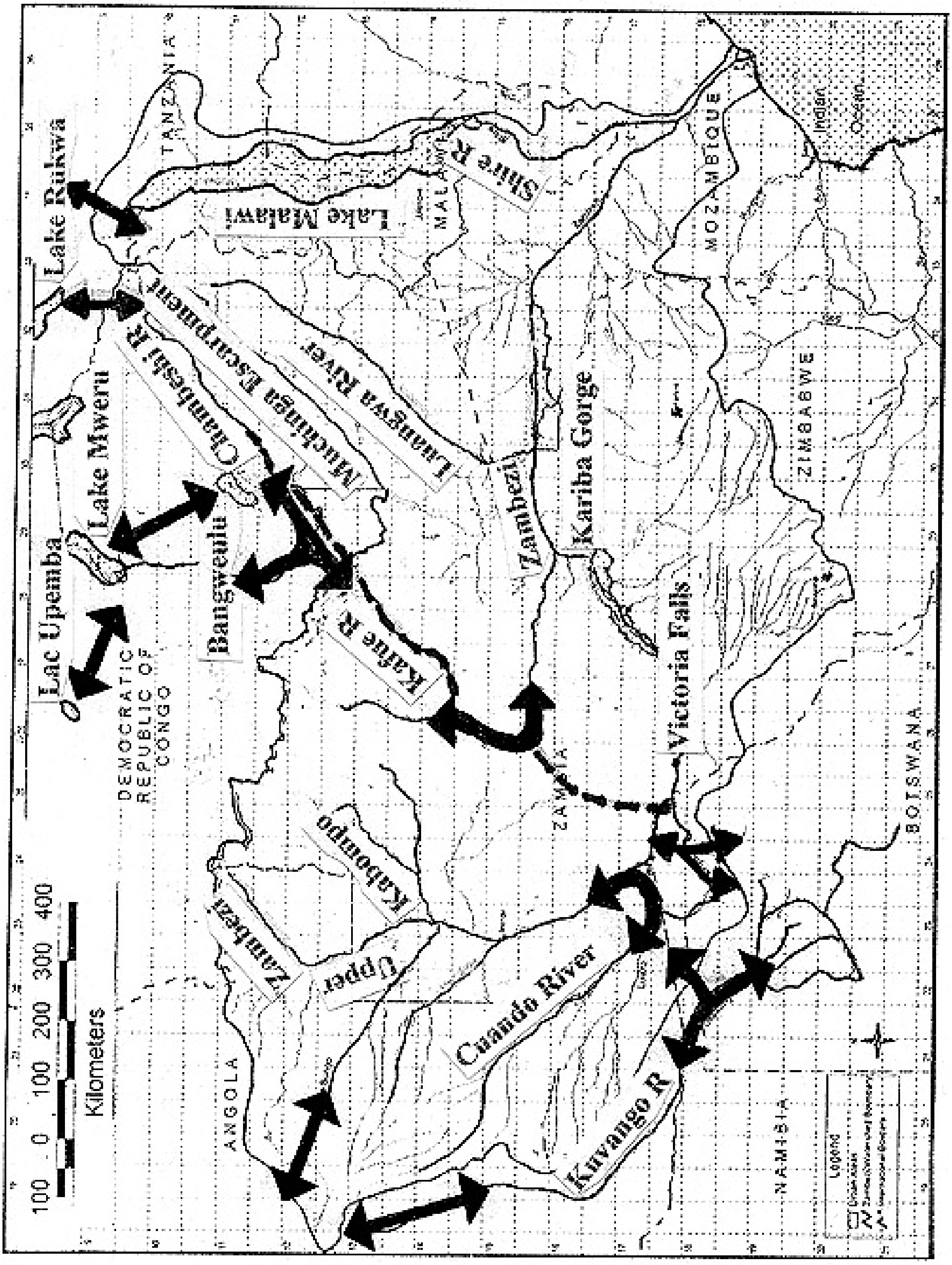
(a) Allopatric speciation followed on formation of the Muchinga Escarpment. This probably resulted in divergence of distinct pairs of species, including *K. crawshayi* and *K. ellipsiprymnus*; *K. vardoni* and *K. senganus*. Modern distributions of Zambian waterbuck suggests that their speciation was comparatively recent – *K. crawshayi* occurs across northern Zambia and southern DRC, but not west of the Zambezi, while *K. ellipsiprymnus* is confined to southern and eastern Zambia, the Luangwa and Middle Zambezi valleys. The two populations are marginally sympatric along the Lusemfwa River, a tributary of the Luangwa (Figure 3.2). The Muchinga Escarpment forms a significant boundary between the larger part of these populations (Ansell 1978, see below).

(b) *Kobus kafuensis* appears to be an allopatric isolate from a more wide-ranging population of *K.* "*leche*", whose descendants today occur only in the Busanga Flats and parts of the Upper Zambezi. In fact, *K. kafuensis* is the only lechwe that occurs marginally south of the present Upper Zambezi drainage system. Its divergence occurred long after capture of the Upper Kafue River by the Middle Zambezi (during the Miocene, Skelton 1994) and most likely as the Kafue Flats became established comparatively recently. A preliminary analysis of lechwe morphometrics (Ansell & Banfield 1980) suggested that *kafuensis* is the most derived, and thus most recent, taxon. Its large horns especially point to the origin of a unique SMRS. As for other populations, the taxonomic status of the Busanga and more westerly populations of *K.* "*leche*" require objective characterization.

(c) The Luapula River captured the Upper Chambeshi in the Pliocene (Dixey 1955, Skelton 1994) and the Bangweulu Basin formed thereafter, but the subsequent timing of changes in drainage patterns in N Zambia is unclear. It was then that *K. smithemani* and *K. robertsi* evolved in N Zambia with the evolution of a distinct SMRS in parapatric or allopatric populations. A likely physical agent of vicariance was tectonic changes across the Mweru and Bangweulu basins (and associated drainage systems) that perhaps influenced the Upemba region of the southern Congo Basin. This caused vicariance of a more contiguous lechwe population(s). It remains to be established which is the daughter species of these populations. The smaller size of *smithemani*, compared to *leche, robertsi* and *kafuensis*, suggests that it is more derived and evolved from an ancestor similar to *robertsi* or *leche*.

(d) There is circumstantial evidence, based on patterns of extant Reduncine diversity, that a separate vicariance event occurred in the E Caprivi across the Chobe, Linyanti, Luiana and Upper Zambezi, perhaps extending beyond north of Sesheke and east of Kazungula. This region corresponds to the boundary between distributions of *vardoni, crawshayi* and *penricei*, and the occurrence of an isolated population of *vardoni*. The taxonomic status of lechwe in the Linyanti and Cuando, as possibly distinct from topotypical *K. leche* in the Okavango Delta and *K. amboellensis* of the Cubango, adds additional, albeit tenuous, evidence. The edges of distributions of species of birds, reptiles and amphibians also correspond to this region. Most pertinently, the biogeographical patterns of reduncine diversity in this region points to the existence of a hotspot of evolutionary divergence.

Figure 3.10. Geographical depiction of the two principal agents hypothesized to have driven diversification of the reduncine antelopes across the Zambezi Basin and its environs since the late Pliocene (~2 Mya). Cross-hatching depicts the Muchinga Escarpment; arrows represent zones of allopatric speciation; thick dashed line represents approximate course of former Chambeshi-Upper Kafue tributary of the Zambezi.



(e) Compared to lechwe, reedbuck and waterbuck are less susceptible to vicariant disturbances as they are not so rigidly dependent on their aquatic habitats. An interesting attribute of the behaviour of puku could be relevant to their biogeography. These antelopes often disperse long distances (Ansell 1978, Ansell & Dowsett 1988), whilst the range of established populations are remarkably stable (as along the Chobe floodplain). Possibility of gene flow across the respective ranges of *vardoni* and *senganus* could have diluted and even obviated vicariant changes to ancestral populations. This behaviour may have camouflaged divergent evolution within these populations, a situation which can only be resolved with genetic studies. It is also significant that Howard (1986a) records long distance dispersal by southern reedbucks in Natal, South Africa.

(f) As already emphasized, it is not possible to distinguish unequivocal divisions between the northern and southern reedbuck (*R. occidentalis* and *R. arundinum*, respectively), should these forms withstand close scrutiny. This problem is compounded by hazy understanding as to where the two forms actually occur within the Zambezi Basin. It is, nonetheless, noteworthy that the boundary between the two forms corresponds (as recognized by Ansell, 1971) to the Zambian plateau where *Kobus* and other clades of vertebrates exhibit recent and considerable diversification. The zone of possible vicariance in *Redunca* may lie in northern Zambia and neighbouring Tanzania, across the headwaters of the Luangwa and Chambeshi rivers extending into the Rukwa depression, where *R. thomasi* (of uncertain taxonomic status) was described from the Songwe River.

(g) Although evidence is vague, a zone of biological diversification across the northeastern edge of the Zambezi Basin is analogous to the E Caprivi. As judged from incomplete data on antelope distributions, this zone would encompass the headwaters of the Luangwa and Chambeshi rivers, and extend north east across the East African rift system into the Rukwa depression. The Rukwa Valley is noted for the occurrence of *K. vardoni*, typically associated with the Upper Zambezi Basin, and both *R. arundinum* and *R. redunca*, at the southern limits of the latter's distribution. An isolated population of lechwe (believed to have been *K. smithemani*) occurred in this area at the northern margin of the Luangwa Valley (Lyell 1913), but is now extinct (Ansell 1971). This complex of reduncine populations likely resulted from recent vicariance associated with tectonic activity in the East African rift.

I suggest that this diversification resulted from a combination of determinants – tectonic events, with these geological and geomorphological processes interacting with climatic changes during the Pleistocene. One candidate is the capture of the Upper Zambezi at Katombora, associated with which were modifications of the drainage of the Chobe and associated system. This had formerly drained southwards into the central Kalahari but was now captured by the Middle Zambezi immediately west of Kazungula. The late Pleistocene was also a time of aridification, when regional climate was cooler and drier. Thus, at least two physical agents likely drove reduncine speciation, and positive feedback could have occurred. The drying-out of wetlands on the Zambezian-Congo Plateau (the African erosion surface) may have activated movement in existing fault systems and so initiated local tectonic activity. In consequence, this may have altered drainage patterns. The result would have contributed to vicariance of wetland biota.

The overall pattern exhibited in reduncine diversification approximates the evolutionary model of punctuated equilibria (Eldredge & Gould 1972). Originally proposed by Eldredge (1971), the punctuated equilibrium model is actually an elaboration, as a temporal analogue, of Mayr's allopatric model of speciation. Following rapid speciation in small vicariant populations, reduncine populations have persisted comparatively unchanged within their ranges. The fossil data available for *Kobus* and *Redunca* also support this model of stasis punctuated by allopatric speciation (Figure 3.1). Following Erwin (1991), the Reduncini are a clade of evolutionarily vibrant lineages that have recently evolved and whose evolution could persist if lineages are not extirpated by human agencies. Their habitats are sites of significant conservation concern given their recent evolution, which has quite possibly involved other biota.

The diversification of Zambezian Reduncini appears to have occurred comparatively recently during the late Pleistocene (Figure 3.1), with their extant diversity resplendent in many closely-related populations (traditionally termed superspecies, Grubb 1978). This is especially true of the lechwes. Their allopatric distributions are possibly a consequence of these antelope's high fidelity to floodplains. I suggest the model that best describes the evolution of Zambezian reduncines is one of species stasis rapidly altered by environmental changes which caused vicariance. This hypothesis is similar to the Turn Over Pulse Hypothesis, which has been used to explain mammal diversification across the continent somewhat earlier in the Tertiary and at much larger scales (Vrba 1985, 1992). Evidence for this is also abundantly represented in fossil record of pigs and primates (including hominids). These corresponded to global fluctuations in climate at the Miocene-Pliocene (5Mya) and Pliocene-Pleistocene (~2Mya) boundaries.

A more detailed model for evolution of Zambezi reduncines is still required, integrating more precise information about geomorphological changes through the Pleistocene into the Holocene. Existing models (notably Skelton 1994 on evolution of fish faunas) are too coarse-grained in their spatial and temporal dimensions, and treat the history of evolutionary change across the Zambezi Basin as proceeding through three linear stages. It was probably not that straightforward, given influences of arid periods and finer-grained vicariance of drainage systems, but this can only be tested with more precise biogeographical analyses using genetic studies of indicator species. Reduncines, especially lechwes are special candidates for finer-grained analysis of this more recent evolution in the region. Studies of their divergence need to be correlated with data pointing to fluctuations in extinct wetlands and those still existing across the basin. I suggest data from carbon deposits in sediments and pollen cores, allied with other palaeoecological research, might aid elucidation of where major lechwe habitats occurred in the comparatively recent geological past.

The susceptibility of reduncine antelopes to these physical modifications of the African erosion surface that forms the Zambezian plateau can only be surmised today. The high habitat fidelity of these aquatic antelopes suggests that the consequences were radical. The response of *K. smithemani* to an abnormal flooding of the Bangweulu area in 1936-1938 illustrates the susceptibility, especially of lechwe, to disruption of their habitats, a susceptibility that introduces the possibility of extinctions. Since species turnover is a function of both extinction and diversification, it is not unlikely that many populations of reduncines declined to extinction when tumultuous events modified wetland habitats. An extremely poor fine-grained fossil record - and remote chances of fossilization - render elucidation of this history difficult from morphological characters. Molecular characters, including construction of gene trees, are the obvious solution, but no matter how complete, can only paint a partial historical chronicle. In this respect, I predict that more detailed studies of the genetic parameters of reduncine diversification will reveal even greater extant diversity than has been pointed out in this review.

3.8 CONSERVATION

Conservation of reduncine antelopes in the Zambezi Basin involves at least three issues. One is the challenge and practice of recognizing and conserving healthy representatives of reduncine species in the region. Much attention has already been paid to this in the review. The second involves the application of scientific knowledge about reduncines to make informed conservation decisions, where reduncine species and the patterns of their evolution are used to indicate sites which support important biodiversity and/or are zones of recent and continuing evolution. Third is the relevance and value of using certain populations of reduncines to support and implement conservation activities. In this latter role, reduncines are flagship or umbrella species. It is important not to confuse these three issues (Caro & O'Doherty 1999). Two or more of these issues might be complementary in a particular conservation project, but they must be teased out and recognized so as to avoid confusion and inappropriate applications.

The reduncines have experienced huge reductions in their population through the 20th century as a result of human depredations. The historical decline of puku in Zambia exemplifies the problem, which has reached its extreme in the extinction of allopatric populations of lechwe (most notoriously *K. robertsi*). Hughes (1933) concluded that puku formed "a thin red line" along the edges of Zambian wetlands, especially vulnerable to hunting, and emphasized that these populations were already suffering major depredations in the early decades of the 20th century. In drawing attention to Hughes' admonition, Vesey Fitzgerald (1961) emphasized that it is these antelopes dependent on open grasslands that are especially prone to human depredation, and cites puku, lechwe and tsessebe as showing huge declines in the ranges and densities of their populations. The case of Kasanka dambo in Kasanka National Park demonstrates that "a thin red line" of puku can be restored with adequate protection.

3.8.1 **Maintenance of populations**

The crux of conserving any species *in situ* is to maintain sufficient habitat. This is the first and obvious step. Any management plan must address the maintenance of viable populations which are not subject to excessive depredation. The disturbance regime (for example the Kafue Flats, Schuster 1980) must be maintained to provide the appropriate cues which determine reproductive and other behaviour. The critical requirements are to reduce human depredation and excessive competition with domestic herbivores. In practice, protected areas of reduncine habitats are essential. As in southern Bangweulu (Thirgood *et al.* 1994), hunting must be prohibited in such core zones, but managed in surrounding buffer and utilization zones.

An important management tool in conservation programmes in Africa is to develop community-based conservation projects, where humans living in and around conservation areas benefit directly from the wildlife therein. It is important to acknowledge that existing programmes remain experiments, and their longevity appears precarious considered against threats of alternative land use practices, and especially unsustainable trends in human population levels.

Kingdon (1982) has emphasized the potential of reduncine antelopes for utilization, as have other authors (East 1989a, 1989b, Grimsdell & Bell 1975). The recovery of lechwe on the Busanga Flats, Caprivi and Bangweulu demonstrate that reduncine antelopes, especially lechwe, can recover rapidly from comparatively low populations. This reproductive potential needs to be considered in conservation management plans for any wetland where they occur, and testifies to considerable chances of success, but only if unsustainable exploitation, unsuitable land use and deleterious habitat modification can be halted.

Research and monitoring has demonstrated that *K. smithemani*, and *K.* "*leche*" on the Busanga Flats (Bell & Grimsdell 1973, Howard & Chabela 1987), have a remarkably high intrinsic rate of population growth. A major determinant of this life history variable is the very high survivorship of neonates coupled with a relatively young age of first reproduction in females. To this high population increase can be added the productive habitat exploited by lechwe (Ansell 1957, Bell & Grimsdell 1972, Grimsdell & Bell 1976, Robinette & Child 1964). Female puku also reproduce at a young age; 66% of calves marked in a study conceived in their first year (Rosser 1987). Howard (1986b) records that fecundity of female southern reedbuck is increased by a post-partum oestrus.

Although many authorities have repeatedly suggested that reduncines, especially lechwe, are suitable for sustainable exploitation, caution is advisable in implementing such programmes. In past centuries, certain African tribes exploited lechwe on a regular basis. Many of these were characterized by coordinated hunts where the antelope were driven with beaters and speared, or captured with dogs. If this historical offtake was sustainable, it is no longer following the introduction of modern hunting technology, national communication systems, and a massive, burgeoning population of rural humans. The consequences have been catastrophic. The exponential declines of lechwe populations in the Caprivi, Kafue Flats and Bangweulu in the past decades speak for themselves. So does the acute reduction in ranges of puku and "red" lechwes from large areas of the Upper Zambezi.

Exploitation of any population can only succeed in the long term if it is tightly managed, such that quotas are adhered to, and the resource is monitored to detect changes and trends in populations. This adds significant costs in the form of skilled personnel and aerial census. It is worth emphasizing that signatories to the Convention on Biological Diversity (to which the riparian states are party) are beholden to perform these activities in the long term within their countries. The large, unique wetlands more than justify this expenditure toward biodiversity conservation. The crux is the commitment and policing of such policies, despite inevitable political changes and burgeoning human demands. Ideally, exploitation of populations of reduncines needs to be coupled with tourism, and with more integrated and thus productive land use. Zambezian wetlands supporting unique reduncine species are especially suited to exclusive, high-paying tourism given the aesthetic attributes of the landscape and other charismatic species, such as Shoebills, in northern Zambia. Alongside sitatunga and shoebills, reduncines are flagship species to attract and maintain conservation support and interest, and in so doing aid development of their habitats as exclusive, international tourist destinations. Economic benefits could be considerable if the resource and the ecological integrity of the landscape is maintained.

3.8.2 **Reduncines as indicator species**

The patterns of diversification exhibited in the reduncine antelopes of the Zambezi Basin provide sober lessons for the assessment of biodiversity. The major part of this review has tried to elucidate the evolution and current taxonomic status of the various populations. The existence of these isolated populations points to the existence of significant wetlands which have persisted through, and also been formed by, significant climatic and tectonic changes. They open up questions about other evolutionary species, especially invertebrates and fishes currently unknown but restricted to the same areas.

The previous section has emphasized that the Reduncini form an evolutionarily vibrant clade of species that might still continue to diverge. Their existence points to a conservation priority in defining conservation areas for Zambezian biodiversity which focus not only on the representation of pattern, but equally on the maintenance of representative landscapes which generated (and continue to maintain) the biodiversity of which reduncine antelopes are part. As Cowling *et al.* (1999) emphasize, the consideration of evolutionary and ecological processes in conservation planning is vital but very challenging, not least because we know so little about these processes.

3.8.3 Reduncines as "umbrella" species in conservation

Like many large mammals, it would appear that a reduncine antelope requires a relatively large ecological neighbourhood in which it can obtain ecological resources to survive and reproduce. This requires designation and maintenance of extensive landscapes. Certain reduncines are popular flagships for conservation in the region. These include the reedbuck of Marromeu and especially the black and Kafue lechwe of Zambia.

The use of any umbrella, or flagship, species needs to be kept within the context of the reality of the overwhelming adversity facing all biodiversity conservation projects. There is a risk that conservation of the target species becomes an overriding rationale for conservation activities and funding. The reality is that the ecological integrity (undeniably a slippery definition in its own right) holds precedence to maintain the habitats where both charismatic and less apparent organisms have evolved and persist. Conservation of reduncine antelopes requires two major investments. One hinges on maintaining their aquatic and surrounding habitats. The second requires reducing human depredations on populations of these antelopes. Ultimately, this requires the synergistic management of all biodiversity and the drainage systems where these biota have evolved.

3.9 CONCLUSIONS AND RECOMMENDATIONS

1. The vicariant patterns of recent diversification in reduncine antelopes render them useful indicators to identify important biodiversity in the Zambezi Basin and further afield. Examples are the occurrence of *K. robertsi* and *K. smithemani* in N Zambia and *K. kafuensis* in the Kafue Flats, both likely to be correlated with recent geomorphological evolution within the Upper Zambezi drainage. Indication of recent evolution and rapid changes in the gradient of biodiversity across certain landscapes are highlighted by changes in reduncine distributions in at least two regions of the Zambezi Basin – the include the E Caprivi and Kazungula, and possibly the headwaters of the Chambeshi and Luangwa extending into the Rukwa Valley of SE Tanzania.

2. The Reduncini comprise a clade of evolutionarily vibrant populations. Their biogeography pointst to zones of recent and on-going evolution. Objectively applied, knowledge of their biogeography and evolution can identify representative and significant landscapes in the Zambezi Basin where evolutionarily significant populations have evolved. As they currently illustrate, the occurrence of fragmented and parapatric populations of reduncines across a large portion of the basin indicates sites for priority assessment and maintenance of aquatic biodiversity in areas where the different species occur. Overall, the pattern and timing of reduncine evolution across the Zambezi Basin indicates that a pulse of diversification has occurred across south-central Africa with special impacts on wetland biodiversity. Available evidence points to this pulse having been recent, rapid and geographically extensive in its occurrence across the Upper Zambezi. Whether caused by tectonic and geomorphological changes, climatic fluctuations, or both, the implications for biology and conservation of a knowledge of its history are profound. The more detailed analysis should be expanded into a search for historical changes in significant wetlands across the modern Upper Zambezi, Chambeshi and Kafue systems and adjacent catchments. Nevertheless, this use of large vertebrates as indicators and surrogates must be applied cautiously in biodiversity conservation

given the gravity of conservation decisions. It is critical to involve other datasets, including those for herpetofauna, fish and especially invertebrates, in a synthesis.

3. Considering their charismatic status and associated public attention, it is indeed surprising that considerable scientific work remains to elucidate the taxonomy of many large Afrotropical herbivores. This deficiency is exemplified in the Reduncini, whose phylogenetic status also requires clarification. A detailed review of the systematics of the Reduncini is required in order to assess and structure conservation planning for all genetically distinct populations. Such a study should include field assessments of existing populations to obtain tissue samples and complete gaps in museum collections.

4. Recent and radical declines, extinctions and growing threats to reduncine antelopes across the Zambezi Basin illustrate an acute conservation crisis. The impacts on most of these large mammals have been extreme, with a sweeping loss of biodiversity across the Upper Zambezi during the 20th century. As exemplified by the lechwe, reduncine antelopes have been lost from huge areas of their original habitats, which have become increasingly dominated by humans and developed for agriculture. It is especially noteworthy that at least one significant population – Roberts' Lechwe, *Kobus robertsi* – has become extinct; an inaccurate taxonomy no doubt contributed to its decline (*K. robertsi* was originally dismissed as an aberrant form of *K. leche*.) The lesson from this example is salutary. Given the great diversity represented among extant reduncine antelope of south central Africa, all discrete populations should be treated as full species with respect to conservation management until their phylogenetic status is conclusively resolved.

5. A field survey of critically threatened reduncine populations is required. This should focus on the southern Congo Basin, eastern and central Angola and, especially, northern Zambia (north of Lake Bangweulu). These surveys cannot exclude the southern Congo Basin and neighbouring Tanzania, and should include an exploration of the former range of *Kobus robertsi* and attempt to establish whether any individuals still persist. The need for this survey is urgent.

6. The potential of reduncine antelopes for controlled exploitation has barely been explored (despite the case of *K. smithemani*). This potential is characterized by their rapid growth rates and high reproductive potential. An adult reduncine antelope yields tasty meat and valuable hides. Males of all species are sought after by trophy hunters. Any such scheme needs to be properly designed and managed by professional ecologists, with conservation of at least one core source area where no cropping occurs. Such schemes are unlikely to succeed in marginal aquatic habitats, or where reduncines compete heavily for forage with other large herbivores.

7. This review has only presented preliminary conclusions. These are actually hypotheses based on incomplete datasets, correlated with equally incomplete historical evidence to provide partial answers to questions of what species of Reduncini occur where, their taxonomy and evolution. Comprehensive and detailed data about reduncine biogeography and diversity (collected and analysed as suggested above) will be invaluable to evaluate and map Afrotropical biodiversity in the continent's wetlands – in the Zambezi Basin, its environs, and elsewhere. These data on such charismatic vertebrates must be meshed with more taxonomically-representative knowledge of the region's biodiversity. The need to understand reduncine diversification and the processes which caused these antelopes and other populations to evolve is important. It points to evolutionary and ecological processes which need to be

maintained, and conceptual tools and datasets to identify representative components of extant biodiversity in the wetlands and other landscapes of Africa.

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