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The Status and Prospects of Wattled Cranes *Grus carunculatus* in the Marromeu Complex of the Zambezi Delta

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Declaration:

This thesis reports the results of original research I conducted under the auspices of the Percy FitzPatrick Institute of African Ornithology, Department of Zoology, University of Cape Town, between 1999 and 2001. All assistance that I received has been fully acknowledged. This work has not been submitted for a degree at any other university.

Carlos T. Bento

Carlos Manuel Bento

To my parents and those who work to save the world's wetlands

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Introduction

Contents

The status and distribution of Wattled Cranes in sub-Saharan Africa

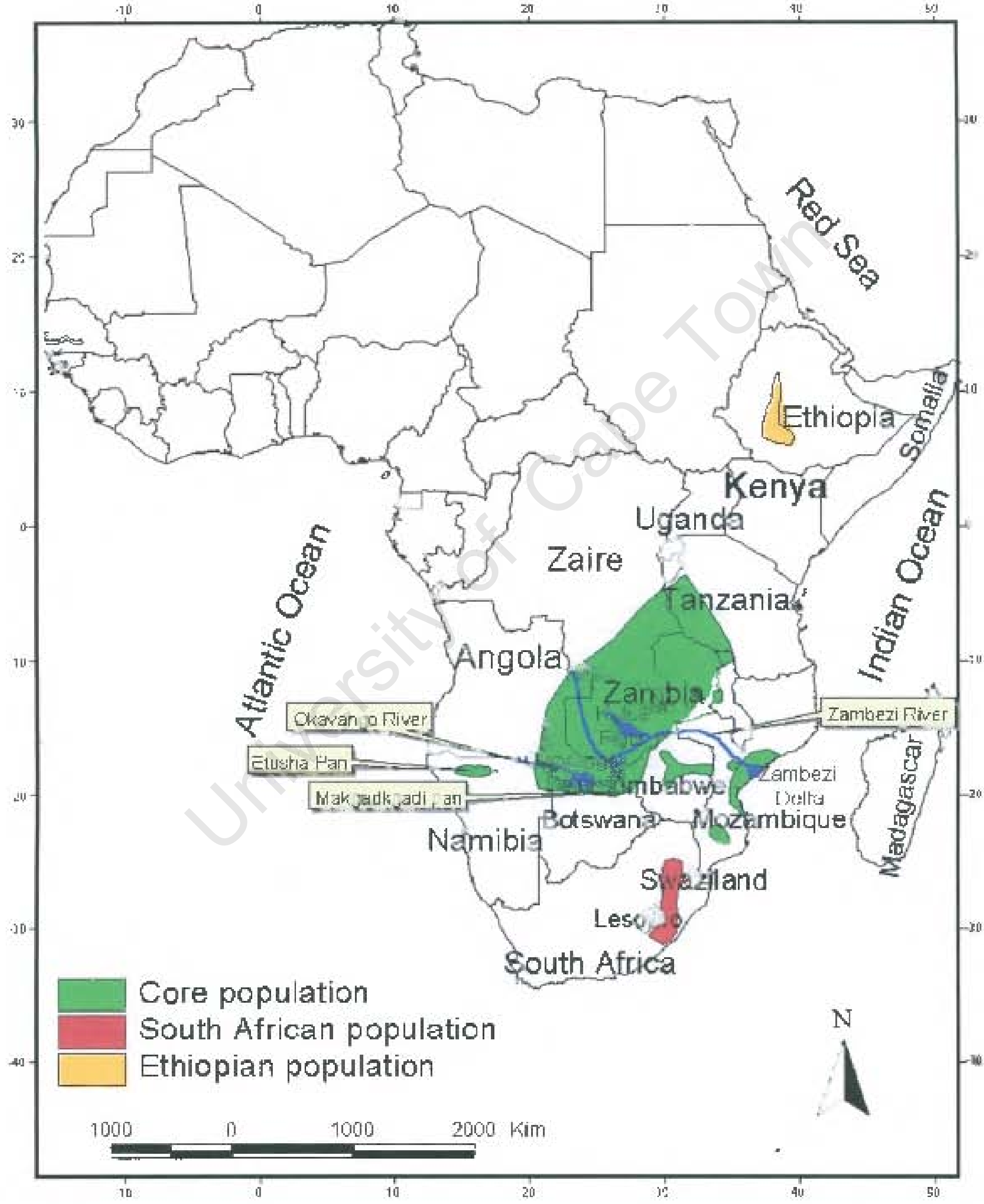
The Wattled Crane *Grus carunculatus* is a globally endangered resident of sub-Saharan Africa (Figure 1.1, Collar and Stuart 1985). The total population of Wattled Cranes is poorly known and estimates vary widely (Table 1.1). In 1985, Urban (1988) estimated the population at about 13 000 - 15 000 birds, while the IUCN (The World Conservation Union) Red Data Book suggested a total population of only 7 000 (Collar and Stuart 1985). Urban (1996) again estimated the total population at about 13 000 – 15 000 birds, but with a markedly different distribution among range countries. Most recently, regional surveys coordinated by the International Crane Foundation and South African Crane Working Group indicate a total population of only about 8 000 birds (R. Beilfuss *in litt.*).

Table 1-1. Estimated populations of Wattled Cranes in Africa, based on status reports by Urban (1988) for 1985 data, Urban (1996) for 1994 data, and recent (2002) unpublished estimates by the International Crane Foundation and Southern African Crane Working Group.

Country	1985	1994	2001
Angola	500?	500?	500??
Botswana	200	1,400-3,500	1,300
D.R. Congo	Several 100s?	100s?	500??
Ethiopia	Several 100s	100s	200
Malawi	100	50	40
Mozambique	250	2,500-2,800	300
Namibia	150	200-300	250
South Africa	300	250-300	235
Tanzania	Several 100s	100s	200
Zambia	11,500	7,000-8,000	4,500
Zimbabwe	Few 100s	250	200
Total	13,000-15,000	13,000-15,000	~8,000??

Three populations are recognized with no subspecies (Figure 1.1). The core population occurs in south central Africa on the primary floodplains and dambos of the Zambezi, upper Congo, and Okavango River basins. This region includes Angola, Botswana, the Democratic Republic of Congo, Malawi, Mozambique, Namibia, Tanzania, Zambia, and Zimbabwe, and there is strong evidence of Wattled Crane movements between these countries (Figure 1.1, Konrad 1981).

Figure1.1. The distribution of Wattled Cranes in Africa.

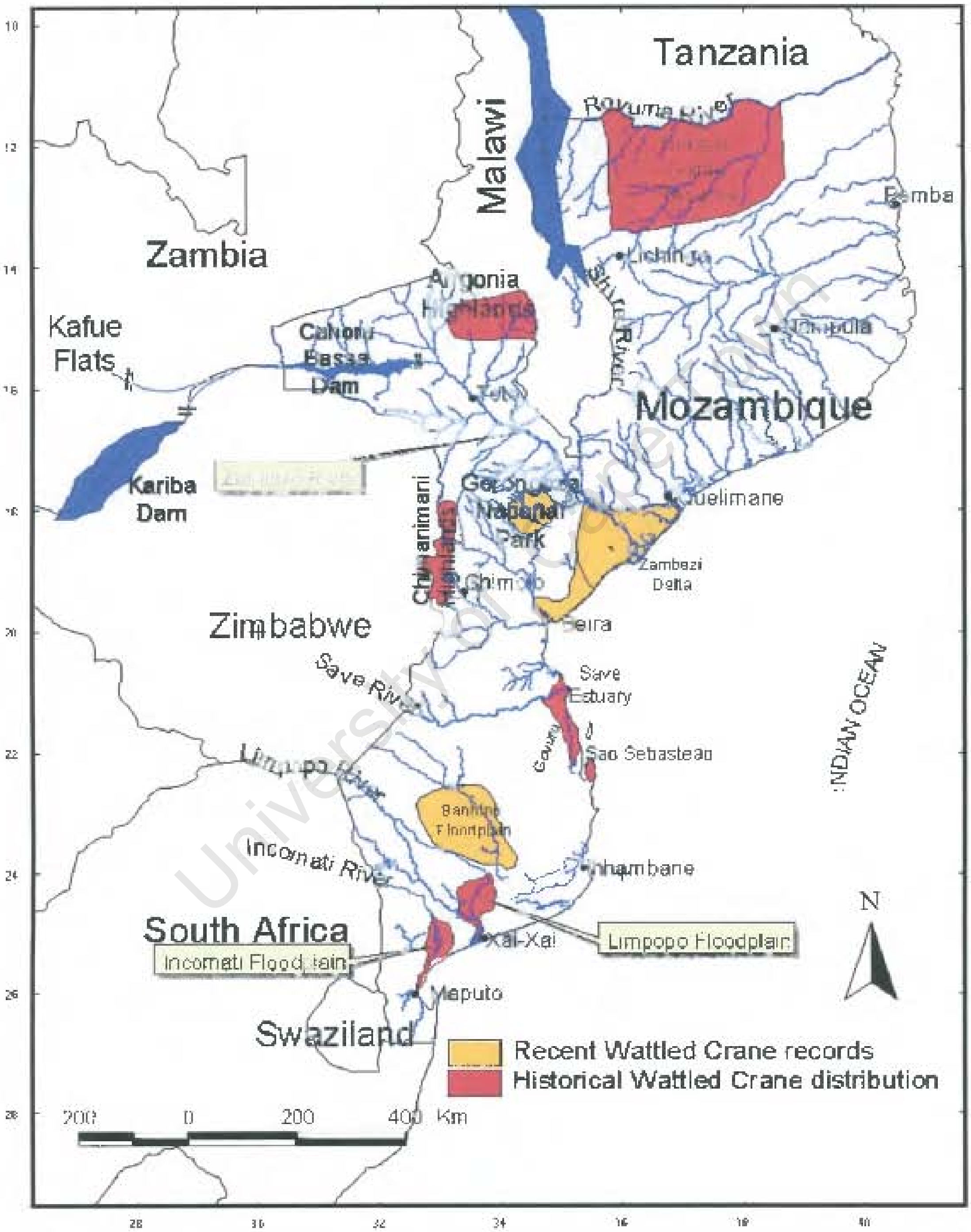


More isolated populations occur in Ethiopia and South Africa, with the Ethiopian population likely to be a separate sub-species (Figure 1.1, K. Jones *in litt.*). Both of these isolated populations are classified as critically endangered (Meine and Archibald 1996).

The population and distribution of Wattled Cranes in Mozambique is poorly known, but historical accounts suggest that Wattled Cranes were previously more abundant and more widespread than today (Figure 1.2, West 1976, 1977, Vernon and Boshoff 1986, 1987, Brooke and Vernon 1988). In central and northern Mozambique, the species was considered to have been "common" in the Zambezi Delta in the 1970s (P. Dutton *in litt.*) and as many as 2500 birds were reported in 1990 (Goodman 1992).

There are historical records of Wattled Cranes on the floodplains of the Zangue River (Gorongoza National Park), Save River, and Rovuma River (Niassa Game Reserve), in the Chimanimani highlands near Zimbabwe, and the Angonia highlands near Malawi (Figure 1.2, West 1976). In southern Mozambique, Wattled Cranes were recorded in Govuru and São Sebasteão coastal grassland (Inhambane Province), Limpopo and Banhine floodplains (Gaza Province), and the Incomati Floodplain (Maputo and Gaza Provinces) (Figure 1.2, Clancey 1970, West 1976). Breeding was suspected in Zambezi Delta and reported in the Save Estuary (Haagner 1948). Today, the only known population of Wattled Cranes in Mozambique occurs in the coastal region between Quelimane and Beira, including the Zambezi Delta, with a few individuals or pairs occasionally reported from Gorongosa National Park and Banhine Floodplain. There are no recent reports from elsewhere in northern and central Mozambique, although many sites have not been visited for decades. The Mozambique Bird Atlas Project (Parker 2000) reported no recent observations of Wattled Cranes from sites where they occurred historically in southern Mozambique.

Figure 1.2. Map showing the recent Wattled Crane records as well as their historical distribution in Mozambique



The status and distribution of the Wattled Crane is of particular conservation concern because of the species' life history traits (e.g. delayed sexual maturity, low reproductive output - Johnsgard 1983) and specialized habitat requirements. The cranes (Gruidae) are the most endangered family of birds in the world, with 11 of 15 species classified as endangered or threatened and with numerous critically endangered sub-species (BirdLife International 2000). Wattled Cranes have the lowest reproductive rate of the world's cranes (Johnsgaard 1983). They produce a 1-2 egg clutch (mean clutch size of 1.6), and rear only one chick per brood (Walkinshaw 1973, Konrad 1981, Mc Cann *et al* 2000). Wattled Cranes reach maturity in their third or fourth year, but typically do not breed successfully until at least 6 years of age (Walkinshaw 1973, McCann *et al* 2000). Their incubation period varies from 33 to 36 days and fledging period ranges from 90 to 130 days - both the longest among the cranes - leaving them vulnerable to fire and predation (Konrad 1981). In Namibia, dry season grass fires frequently kill small chicks and wetland fires threaten breeding activity (Hines 1996).

Wattled Crane productivity is also low because many pairs do not nest annually (Konrad 1981). Nesting pairs require wetlands with minimal human disturbance and may defend territories of up to one square kilometre: small wetlands therefore often support only one pair (Konrad 1981). Within their territories, Wattled Cranes restrict their nests to shallow flooded areas where water depths are sufficient to prevent the depredation of eggs and chicks (Douthwaite 1982). They typically begin nesting as flood waters recede, both to reduce the risk of nest submergence and to take advantage of the flush of food resources associated with flood recession (Konrad 1981). When hydrological conditions are not satisfactory at a particular location due to extreme drought, flooding or inappropriate water management, most Wattled Cranes fail to initiate nesting

(Douthwaite 1974).

The Wattled Crane also has a very specialized diet that greatly limits the extent of available feeding habitats. More than 98% of all foraging activity involves digging for the tubers and rhizomes of *Cyperus* spp. and *Eleocharis* spp. sedges and *Nymphaea* spp. waterlilies, usually in shallow standing waters (Douthwaite 1974, Konrad 1981). Sarus Cranes *Grus antigone* in Vietnam (Duc *et al* 1989) and Brolgas *Grus rubicundus* in Australia (Lavery and Blackman 1969, Blakers *et al* 1984) have a similar dependence on wetland sedges. Tuber production by *Eleocharis* spp. depends on an annual cycle of flooding and drying (Frith and Davies 1961). When floods fail or wetland sites become permanently inundated, tuber productivity decreases and the sedges eventually disappear. Wattled Crane chicks further require a protein-rich diet of insects, frogs, and occasionally fish until they are able to probe for tubers (Konrad 1981). Typically, Wattled Cranes graze in association with large mammals, especially Red Lechwe *Kobus leche*, that graze on the floodplain vegetation and thus allow the cranes easy access to underground resources (Douthwaite 1974).

Wattled Cranes are the most wetland-dependent of the African cranes (Meine and Archibald 1996). From the smallest highland dambos to the vast floodplains of major river systems, wetlands in sub-Saharan Africa are threatened by a variety of human activities including dams, water diversions, agricultural development, overgrazing, deforestation and agrochemical pollution (Hughes and Hughes 1992). Perhaps nowhere in Africa are such threats more grave for Wattled Cranes than in the Zambezi Delta of Mozambique.

The Zambezi Delta

The Zambezi Delta is located adjacent to the Indian Ocean coast of central Mozambique between 18°00'S; 35°00'E and 19°00'S; 36°05'E. The Delta is triangular in shape, covering an area of approximately 12 000 km² that stretches 120 km from its northern inland apex at Mopeia to the Zambezi mouth, and 200 km along the coastline south from Cuacua River outlet near Quelimane to the Zuni River outlet (Figure 1.3). The Delta is bordered to the north by the Morrumbala escarpment that serves as a divide between the Zambezi and Shire River catchments, and to the west by the Cheringoma escarpment that separates the Zambezi and Pungue River catchments (Figure1.3). Most of the Delta is extremely flat and poorly drained, with widespread areas underlain by hydromorphic vertisols and gleys that support a variety of wetland plant communities (Beilfuss *et al* 2000, Beilfuss 2002).

The Zambezi Delta is a wetland of international importance for wildlife including Cape Buffalo *Syncerus caffer*, Common Waterbuck *Kobus ellipsipymnus*, Sable Antelope *Hippotragus niger*, Lichtenstein's Hartebeest *Sigmoceros lichtensteinii*, Burchell's Zebra *Equus burchellii* and African Elephant *Loxodonta africana*. Waterbirds of international conservation concern in the Delta include the Wattled Crane, Grey Crowned Crane *Balearica regulorum*, African Skimmer *Rynchops flavirostris*, Great White Pelican *Pelecanus onocrotalus*, Pink-backed Pelican *P. rufescens*, Woolly-necked Stork *Ciconia episcopus*, Abdim's Stork *C. abdimii*, African Openbill *Anastomus lamelligerus*, Saddle-billed Stork *Ephippiorhynchus senegalensis*, Yellow-billed Stork *Mycteria ibis*, Collared Praticole *Glareola pratincola* and Caspian Tern *Sterna caspia* (Beifuss and Allan 1996, Beilfuss and Bento 1998). The Delta's coastal mangroves support one of the largest breeding colonies of Pink-backed Pelicans *Pelecanus rufescens* in southern Africa (Goodman 1992).

Large mixed-breeding colonies of herons, egrets, storks, and cormorants have also been recorded (Beilfuss and Bento 1998). The Delta is also home to hundreds of thousands of farmers and fishermen who depend on the floodplain for their livelihoods. Extensive coastal mangroves and estuaries support a productive prawn fishery (Hoguane 1997). Because of its rich biodiversity and economic importance, the Delta is a candidate for designation as a *Wetland of International Importance* under the Ramsar Convention (Davis 1994).

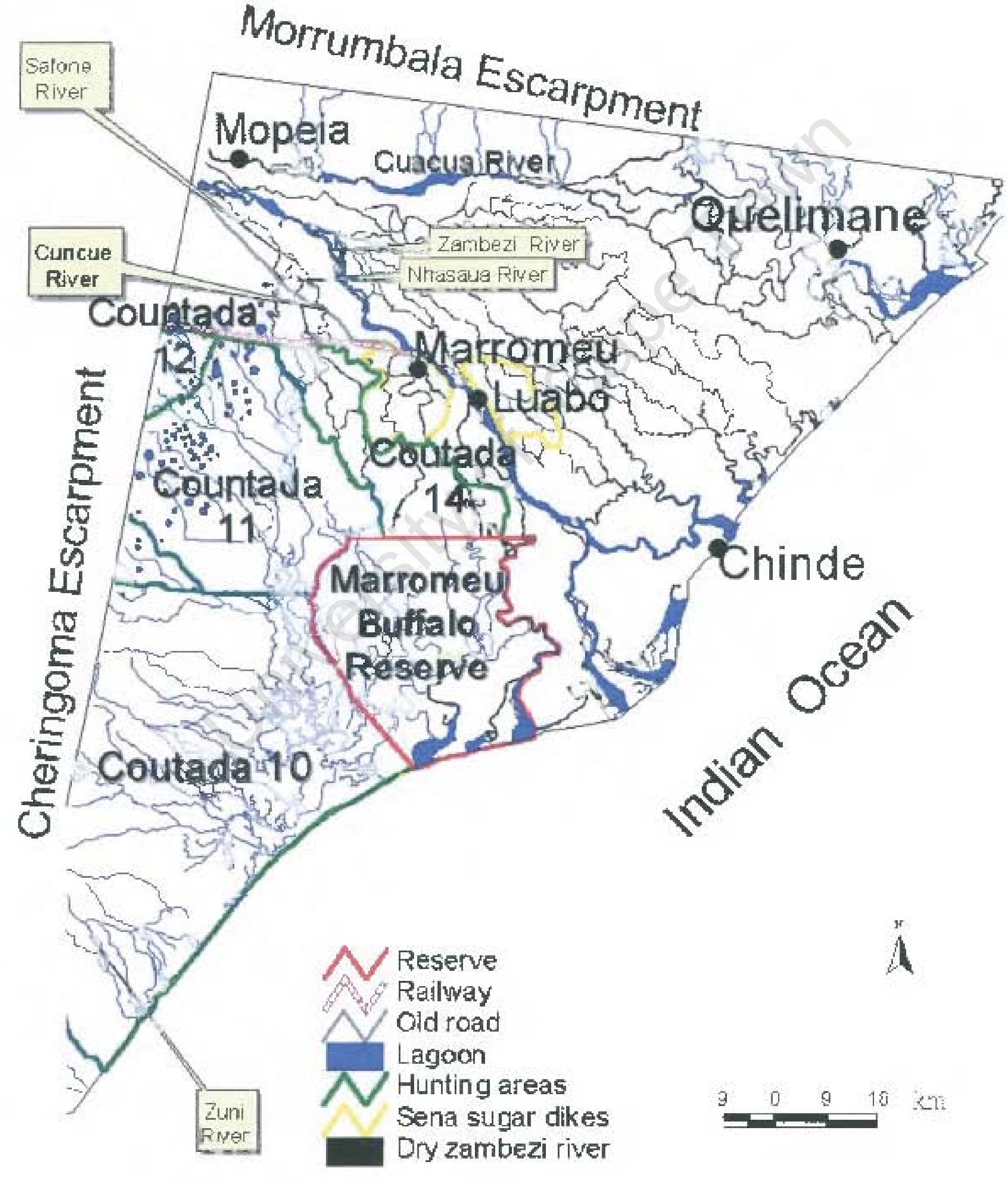
Wattled Cranes occur on the south bank floodplains of the Zambezi Delta in an area known as the Marromeu Complex. The Marromeu Complex comprises the protected Marromeu Buffalo Reserve (*Reserva especial de Marromeu*) and four surrounding hunting concessions (*Coutadas* 10, 11, 12, and 14) in northern Sofala Province (Anderson *et al* 1990) (Figure 1.3). The Complex includes more than 688,000 ha. of dry forest and woodland, savanna, floodplain grassland, deep-water swamp, coastal dune and mangrove forest. The Quaternary Deltoid Plain underlies the core floodplain areas and supports vast expanses of open floodplain grassland and shallow swamps on a mosaic of clay, clay loam, and organic silt soils (Loxton Hunting and Associates 1975). Zambezi floodwaters are distributed to the plains through an intricate network of recent alluvial channels cut into the deltoid plain, most important of which are the Salone, Cuncue, and Nhausau Rivers with associated levees and backwater pans. At the western margin of the deltoid plain, the Cheringoma escarpment of the Limpopo Surface rises gradually at 3°-5° to a height of 394 m amsl, where it forms the eastern side of the Rift Valley (Tinley 1977). The plateau is composed of Cretaceous and Tertiary limestones, overlain by Quaternary sands (Tinley 1977). The Mungari, Ruave, Sanga, and Zuni Rivers drain from the Cheringoma escarpment, fanning out in a series of outwash plains of alluvial sand fans along the western edge of the Zambezi Delta. The total catchment area of the Cheringoma escarpment draining to the Marromeu Complex is approximately 8,300 km^2 (Beilfuss 2001, in review).

Two distinct seasons occur in the region, a wet season and a dry season, as influenced by the movement of the Inter-tropical Convergence Zone (ITCZ). The main rainy season usually occurs over a 4-6 month period between October and April, and is characterized by brief periods of thunderstorms followed by periods of drier weather. Mean annual rainfall ranges from 1000 mm near Mopeia to more than 1400 mm at Quelimane, and there is a considerable inter-annual variation (Beilfuss 2001, in review).

At the onset of the rainy season, local rainfall saturates the low-lying soils of the Marromeu Complex. As the rainy season continues, runoff from the Cheringoma escarpment further inundates the floodplains along the western perimeter of the Delta, filling shallow lakes and lagoons. Deep and prolonged inundation of the vast Marromeu floodplains occurs when the Zambezi River overtops its banks (typically during the peak flooding months of February and April) and spreads laterally across the Delta and through the main channels (Davies 1986, Beilfuss 2001, in review).

Surface waters are subsequently lost through seepage and evapotranspiration during the dry season. Drought years may result in minimal runoff and accumulation of surface waters at the base of the Cheringoma escarpment, leaving the floodplain grasslands dry for most of the year. Alternatively, years of extreme rainfall may result in deep and prolonged inundation of the floodplain for up to six months, independent of Zambezi floodwaters (Beilfuss 2001).

Figure1.3. Map of the Zambezi Delta showing the Marromeu Buffalo Reserve and four hunting units.



Historical and present water regimes

Over the past century, natural flooding processes in the Marromeu Complex have been severely disrupted by the construction of upstream dams on the Zambezi River as well as by the construction of roads, railways, and flood protection dykes in the Delta. A detailed study of hydrological change is beyond the scope of this thesis, but several studies have analyzed long-term patterns of hydrological change in the Lower Zambezi catchment in depth, including Rendel Palmer and Tritton (1979), Bolton (1983), Davies (1986), Sushka and Napica (1988), and, most notably, Beilfuss (2001) and Beilfuss and dos Santos in review). I summarize the key points from these and other studies below as they relate to understanding the impacts of hydrological changes in the Zambezi Delta.

Historically, the hydrological regime of the Zambezi Delta was primarily determined by the cumulative, unregulated runoff of the Upper, Middle and Lower Zambezi Catchments. The Upper Zambezi drains from the headwaters in northwestern Zambia to Victoria Falls, and has a mean discharge of 1044 m^3/s (Beilfuss 2001, Beilfuss and dos Santos in review). Peak flood flows from the Upper Zambezi catchment are partially attenuated by the vast Barotse Plain (Reeve and Edmonds 1966). From Victoria Falls through Kariba Gorge to Cahora Bassa Gorge the Zambezi River drains the Middle Zambezi catchments (Balon and Coche 1974). With the exception of the Kafue River catchment, the Middle Zambezi catchment has few significant floodplains and runoff occurs rapidly during the rainy season relative to the Upper Zambezi catchment. Differences in runoff patterns between the Upper and Middle Zambezi catchments result in a bimodal flooding pattern along the Zambezi River, with an early flood locally known as "Gumbora" from the Middle catchment and the major annual flood known as

"Mororwe" from the Upper catchment (Davies 1986). The mean runoff into Cahora-Bassa Gorge is 2494 m³/s, with peak floods discharges generally in February-March (Beilfuss 2001, Beilfuss and dos Santos in review). Below Cahora-Bassa Gorge, the Zambezi receives runoff from several rapidlydraining tributaries, most notably the Luia, Revuboe, and Luenha Rivers. The largest tributary of the Lower Zambezi catchment, the Shire River, enters the Zambezi approximately 40 km upstream of the apex of the Zambezi Delta. The estimated average Zambezi runoff volume reaching the Delta is 3424 m³/s (Beilfuss 2001, Beilfuss and dos Santos in review). This runoff is supplemented by local runoff from the Morrumbala and Cheringoma escarpments that border the Delta (Figure 1.3).

Floodwaters are spread across the Zambezi Delta through a complex channel network (Beilfuss 2001, Beilfuss and dos Santos in review). Near the Delta apex at Mopeia, the Cuacua River splits off from the Zambezi, collects runoff from the Morrumbala escarpment, and spreads over the northern bank of the Delta (Figure 1.3). Further downstream, three major tributaries - the Salone, Cuncue and Nhasaua Rivers - split off to the southern bank (Figure 1.3). The Salone River runs along the west edge of Delta floodplain, collects runoff from the Cheringoma escarpment, and discharges into the northwestern portion of the Marromeu Complex (Figure 1.3). The Cuncue River spreads its waters into the northern portion of Marromeu Complex, and the Nhasaua River discharges into the eastern portion of Marromeu (Figure 1.3). Historically, these Zambezi distribution channels began discharging to the Delta Floodplain when flows in the Zambezi River exceeded 4500m³/s (Beifuss 2001, Beilfuss and dos Santos in review).

The degradation of the Zambezi Delta's hydrological system began as early as

1893, when low dykes were built to protect the sugar cane plantations at Mopeia (Figure 1.3). These dykes blocked the upper Delta distribution channels that previously flooded the northern bank floodplain (Beilfuss 2001, Beilfuss and dos Santo in review). Similar flood protection dykes were also built at Luabo and Marromeu (Figure 1.3). In 1926, the dykes were raised and strengthened, and have been overtopped only five times since, in 1939, 1940, 1952, 1958 and 1978 (Bolton 1983).

In the 1930s, a railway and road were constructed between Marromeu and Sena (80 km upstream); these further obstructed the passage of water into the upper channels between Mopeia and Marromeu (Tinley 1994). Water movement in this region was additionally restricted during the 1970s by the construction of a railway line between Marromeu and Inhamitanga on the Cheringoma escarpment. The cumulative impact of these road and dyke works has been a significant reduction in the movement of floodwaters between the Zambezi River and Marromeu Complex (Beilfuss 2001, Beilfuss and dos Santos in review).

Over the past 40 years, the impact of these dykes, roads, and railways has been greatly exacerbated by the construction of large hydroelectric dams on the Zambezi River. In December 1958, Kariba Dam, the first major dam on the Zambezi River, began impounding water and further altered flooding patterns in the Delta. Kariba Dam controlled more than 40% of the total Zambezi runoff and was operated to generate steady hydroelectric power by storing peak flood water and releasing a constant outflow of water (Reeve and Edmonds 1966). Kariba has reduced peak floods volume in March by 36%, and in April by 41%, relative to pre-dam conditions (Beilfuss 2001, Beilfuss and dos Santos in review). During the 1960s and 1970s, a major tributary of the Middle Zambezi, the Kafue River, was dammed, first at Kafue Gorge and then at Itezhitezhi Gorge, further stabilizing the Zambezi flow regime downstream of Kariba (Balasubrahmanyam and Abou-Zeid 1982, Turner 1984).

The control of the Zambezi River culminated in December 1974 with the completion of Cahora Bassa Dam. Cahora Bassa Reservoir regulates the Zambezi River flow for hydropower production, and since completion of the dam the natural flood cycles of the Zambezi River have been fundamentally changed. During years of low to average runoff in the Zambezi catchment, Cahora Bassa discharges almost constant flow throughout the year (Beilfuss 2001, in review (b)). Inundation of the Marromeu Complex, when it occurs, is now dependent on local runoff from the Cheringoma escarpment or on very high volume, short-duration water releases from Cahora Bassa to protect the dam wall during years of exceptional flooding in the upper basin (Beilfuss and Davis 1999). Mean monthly flows have decreased by 64% during the peak flooding months of February, March, and April, and by 45% during January and May. By contrast average monthly flows in November are four times greater than their were historically (Beilfuss 2001, Beilfuss and Bento in review). Cahora Bassa directly reduces inflows by 46% during the peak flooding months of February and March, and by 20% in January and May (Beilfuss and Bento in review).

The reduction in peak flows and increase in dry season flows have resulted in degradation of the main Zambezi channel. The riverZambezi has downcut below its distributary channels in the Delta, further reducing the spread of floodwaters into the Delta (Davies *et al* 2001). The minimum flood level required to overtop and discharge through its distributaries is approximately 4500 m^3/s, a level that rarely occurs in the regulated Zambezi but which occurred in most years prior to regulation (Beilfuss 2001, Beifuss and Santos in review). The cumulative effect of Zambezi regulation and associated physical changes is a reduction in the magnitude, duration, and extent of flooding in the Delta.

These changes confirm the fears of Davies *et al.* (1975), Hall and Davies (1974), and Tinley (1975), who predicted that Cahora Bassa Dam would result in severe hydrological degradation of the Zambezi system. They predicted numerous social and ecological consequences of these hydrological changes, including reduced coastal and riverine fisheries, increased coastal erosion, reduced coastal mangrove communities, reduced silt deposition, increased salt water intrusion, reduced primary productivity, and the replacement of open floodplain grassland vegetation by upland shrubs and trees. Subsequent research has shown that many of these changes have occurred. For example, Gammelsrod (1996) and Hoguane (1997) studied the effect of Zambezi River management on the prawn fishery of central Mozambique, establishing that prown abundance is directly related to Zambezi runoff patterns and that regulation by the Cahora Bassa Dam has resulted in a loss of $10-20 million per annum. Oral history studies by the University of Eduardo Mondlane and others (Beilfuss *et al* 2002) documented the reduced value of artisinal fisheries and flood recession agricultural practices in the lower Zambezi. The drying of the floodplain has resulted in widespread and significant changes in the major vegetation communities of the Delta, including facilitating the invasion of woody species into floodplain grasslands, the displacement of flood-tolerant species by more upland species, and the displacement of freshwater vegetation by salt-tolerant species (Beilfuss *et al* 2000, Beilfuss *et al* in review). The drying conditions have opened the area to aggressive poaching of wildlife, with a more than 90% reduction in all major grazing species during the civil war from

1977 to 1992 (Anderson *et. al* 1990, Tinley 1994). Fires now annually consume most of the Delta grasslands during the dry season.

Davies *et al* (1975) also predicted that hydrological changes would result in the disruption (or mistiming) of reproductive patterns of wildlife. To date, no research has evaluated this prediction. If true, such changes could be catastrophic for the Wattled Cranes of the Zambezi Delta because of their life history characteristics. The goal of this thesis is to determine whether hydrological changes in the Zambezi system have affected the breeding success of Wattled Cranes in the Zambezi Delta.

Thesis outline

This thesis investigates the population status, distribution, and ecology of Wattled Cranes in the Marromeu Complex, with the aim of assessing the impacts of hydrological and ecological changes on the breeding and feeding ecology of the birds. I hypothesize that Wattled Crane breeding success is low in the Marromeu Complex compared to other less disturbed wetlands in southern Africa because of changes in hydrological conditions (and associated changes in patterns of fire and grazing). I also hypothesize that within the Marromeu Complex, breeding success is lower in areas where hydrological conditions are most altered and higher in areas where the conditions are least changed. Third, I hypothesize that efforts to improve the carrying capacity of the Marromeu Complex through hydrological management will increase the viability of the Marromeu population and benefit the regional population of Wattled Cranes.

In Chapter 2, I assess the distribution and abundance of Wattled Crane in the Zambezi Delta. In Chapter 3, I investigate the biology of the sedge *Eleocharis* and how it affects the Wattled Cranes on a seasonal basis. In Chapter 4, I develop a simulation model of the Wattled Cranes' population dynamics to determine whether management is necessary to maintain the population. Conclusions and recommendations of the study are summarized in Chapter 5.

Chapter II: The distribution, population trends and population structure of Wattled Cranes in the Zambezi Delta.

Contents

Introduction

No historical data exist on either the population size or distribution of Wattled Cranes in the Zambezi Delta. The hydrology of the Delta has been profoundly altered over the past century due to the effects of upstream impoundments (Chapter I). Wattled Cranes, however, still breed in the Delta, providing a good opportunity to study how they have adapted to these changes (Beilfuss and Allan 1996).

The most significant changes to the Delta's hydrological regime have arisen as a result of the hydro-electric schemes at Kariba and Cahora Bassa dams (Chapter I). The dams reduce the river flow during the rainy season and increase it during the dry season through controlled releases. Damming has reduced the size of the floodplain and consequently has reduced suitable breeding and feeding areas for Wattled Cranes as seasonally wet habitats have become increasingly dry. Most of the Delta is now dry throughout the year and is burnt annually. Prior to dam construction, the Delta was inundated for more than 9 months of the year (Beilfuss and Allan 1996).

The movements of Wattled Cranes are poorly understood. Almost certainly movement is stimulated by water level, occurring both when conditions are locally dry and when extreme local flooding fully inundates otherwise suitable habitats. Wattled Cranes move away from the Kafue Flats in Zambia during low rainfall years, possibly joining the Okavango Delta and Makgadikgadi Pan populations in Botswana. Additional movements might occur between Bangweulu Swamp, the Kafue Flats, and other wetlands along Zambezi Basin when water levels are unusually high. Wattled Cranes might move to the Zambezi Delta when conditions are unfavorable elsewhere (Meine and Archibald 1996).

Given that changes to the hydrology of the Zambezi Delta have almost certainly reduced the availability of suitable habitat for Wattled Cranes, this study had the following objectives:

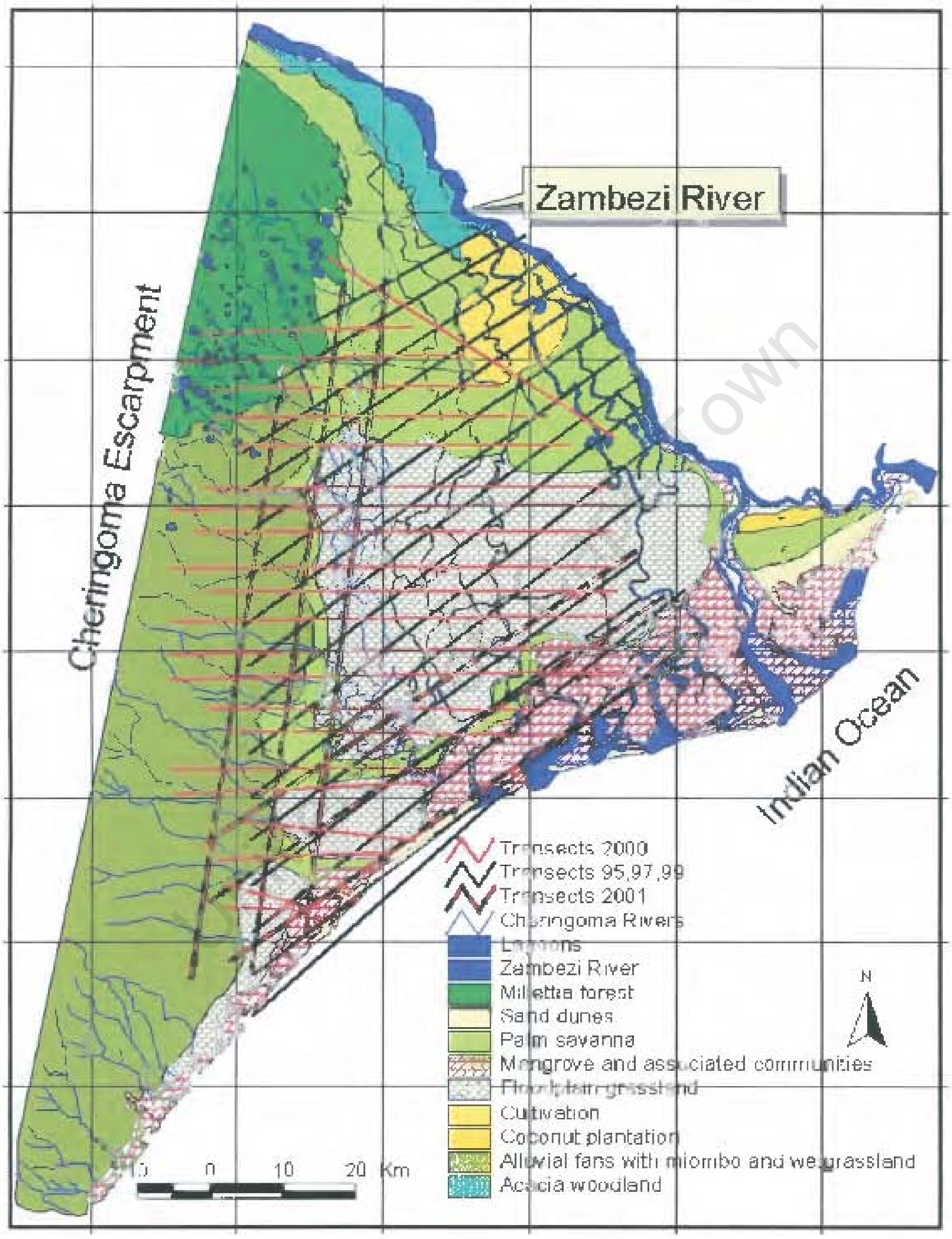
1) To assess the distribution and abundance of cranes in the Delta over a 5-year period (encompassing both wet and dry seasons); and
2) quantify inter-annual variation in the cranes' population structure as an indication of how variation in rainfall influences breeding effort and breeding success.

Methods

Aerial Surveys

Six aerial surveys were conducted during the study period. Surveys targeted either the end of the wet season (March-May) when it was predicted that the maximum number of pairs would be establishing territories, or the latter part of the dry season (November) when chicks are large enough to see from the air. In 1995, 1997 and 2001, surveys were conducted at the end of wet season. In 1999, 2000 and 2001 transects were flown at the end of the dry season. All surveys were flown in a six-seater Cessna 210 with two observers located on each side of the plane (the April 2001 survey was flown in a Piper Super Cub with a single observer. Transect lines were orientated approximately parallel to the coast (Figure 2.1). Surveys were flown 90 m above ground level at an average speed of 100 knots (177 km/h). An in-cockpit Global Positioning Satellite System (GPS) was used to identify the precise locations of cranes. The 17 transects flown on each survey were 4 km apart and achieved an estimated coverage of 50% of the entire floodplain. The locations and lengths of each transect are summarized in Figure 2.1.

Figure 2.1. Locations of transects flown in 1995-1999 and 2000-2001.



Surveys were centred on the floodplain grassland habitat between the Zambezi River in the east and the ecotone between the Delta and miombo woodland in the west.

Each observer recorded data with a tape-recorder. During the survey all Wattled Cranes observed were counted as singletons, pairs or flocks. Pairs were further categorized as (a) pair with chick, (b) pair nesting and (c) pair with no evidence of breeding activity.

In addition, the main habitat type and wetland vegetation were recorded at all locations where cranes were seen. Large flocks were circled at lower altitude to determine whether birds were adults or juveniles (as distinguished by head plumage).

Based on the 1995-1999 surveys it was clear that most Wattled Cranes were located near the Cheringoma escarpment where the floodplain is inundated by the overtopping of seasonal rivers flowing down from the Cheringoma Plateau. Thus, in 2000 and 2001, surveys concentrated more heavily on the Cheringoma area, including both floodplain and escarpment. Transects were orientated East-West and North-South (along the miombo ecotone, Figure 2.1). Each survey comprised 22 transects (4 km apart). The total coverage was ca 60% of the whole floodplain. Surveys were all flown at 90 m above ground level and the data recorded were identical to those collected in 1995-1999.

The basic vegetation map of the Zambezi Delta was obtained from Landsat 7 ETM image dated 16 July 2000 from the United States Geological Survey (USGS). The image was received geo-referenced from the International Crane Foundation GIS-Lab. The vegetation was classified by digitalizing manually from a computer screen with Arc View GIS software.

The ditribution of *Eleocharis* was obtained by recording GPS coordinates of the plant's occurrence during the 1999-2001 aerial surveys. All points were plotted on the basic vegetation map and *Eleocharis* sp. occurrence was drowned.

Ground Survey

Ground surveys were undertaken to locate Wattled Crane feeding areas and identify the plants and parts of the plant on which the birds were feeding. The survey was limited to the edge of the Delta floodplain at Coutadas 10 and 11 (Chapter I) due to the inaccessibility of the remaining area. The Savana River Floodplain ground survey took place along the Savana Road which links Beira Town and the Savana River.

Data analysis

From 1995-1999 and in 2001, aerial surveys covered 50% of the Delta. Numbers of pairs and single birds recorded were thus doubled to estimate the population size. Flocks were not treated in the same way and numbers were simply added to the estimated numbers of pairs and singletons. This gives a minimum estimate of the number of cranes on the floodplain. In 2000, the calculation followed the same procedure, correcting for a survey coverage of 60%. The number of chicks was based on the number of chicks observed, corrected for coverage. Because Wattled Cranes were associated exclusively with the wetland plant *Eleocharis* (Chapter 3), calculations of adult density were based on the total area of *Eleocharis*. The annual number of chicks per breeding pair was calculated based on the ratio of observed chicks to observed pairs. The annual production of chicks per potential breeding pair was calculated based on the above ratio and the potential breeding population of the Zambezi Delta, defined as the maximum number of pairs seen on any survey.

Results

Distribution and density

The combined results of all six surveys between 1995 – 2001 (Figures 2.2 - 2.4) provide an over view of Wattled Crane distribution along the base of the Cheringoma Plateau and the coastal floodplain. The soil in the latter area is saline and is influenced by tides. The occurrence of cranes near the coast is restricted to seasonal floodplain grassland where there are patches of *Eleocharis* sp.. This wetland sedge is closely associated with seasonal rivers flowing down from the Cheringoma Plateau. *Eleocharis* sp. is also found, but sparsely, in the few remaining areas where the Zambezi River overtops onto the floodplain. Most of this historical floodplain area is now dry. *Eleocharis* sp. is also found in areas under the influence of the Zambezi River and immediately inland of the mangrove communities. Very few Wattled Cranes were observed in areas of the Delta lacking *Eleocharis.* (Figure 2.2 -24).

A comparison of the 1999, 2000 and 2001 aerial surveys shows that, although on all surveys Wattled Cranes were confined to the base of the Cheringoma Planteau and parts of the coastal floodplain, the distribution changed slightly between years. In 1999, Wattled Cranes were concentrated in the central sections of the Cheringoma *Eleocharis* beds, with few occurring on the coastal plain (Figure 2.2). Very few Wattled Cranes were observed on the *Eleocharis* belt influenced by the Zambezi River.

The 2000 aerial survey showed the same association between cranes and *Eleocharis* (Figure 2.3). As in 1999, only one pair (with one chick) was observed on the *Eleocharis* belt under the influence of the Zambezi River. In the *Eleocharis* habitats under the influence of the Cheringoma rivers, Wattled Cranes were centred farther west (i.e. closer to the escarpment) and were more dispersed than during 1999, suggesting that the distribution of suitable habitat differed between the two years.

Figure 2.2. The November 1999 Wattled Crane Distribution.

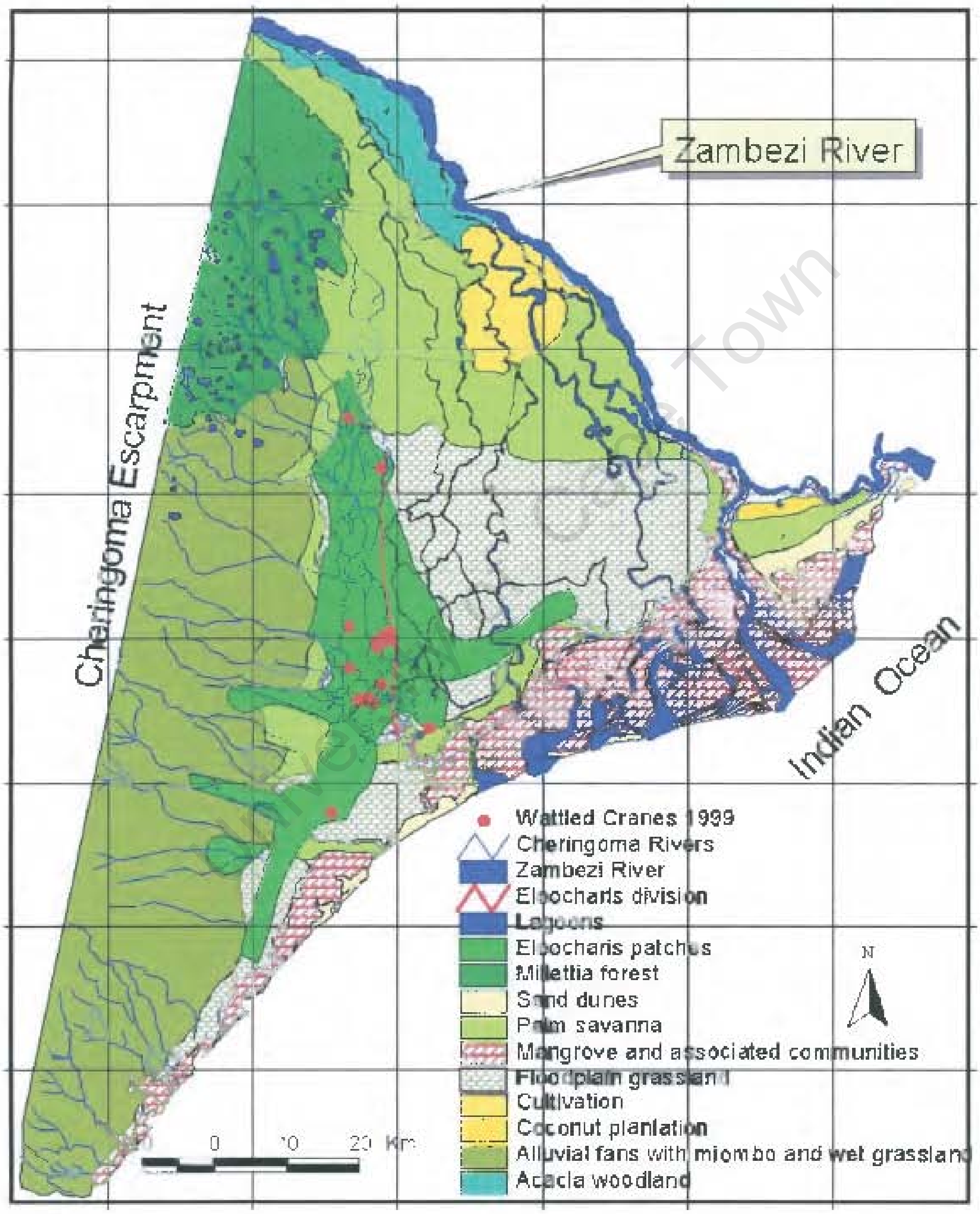
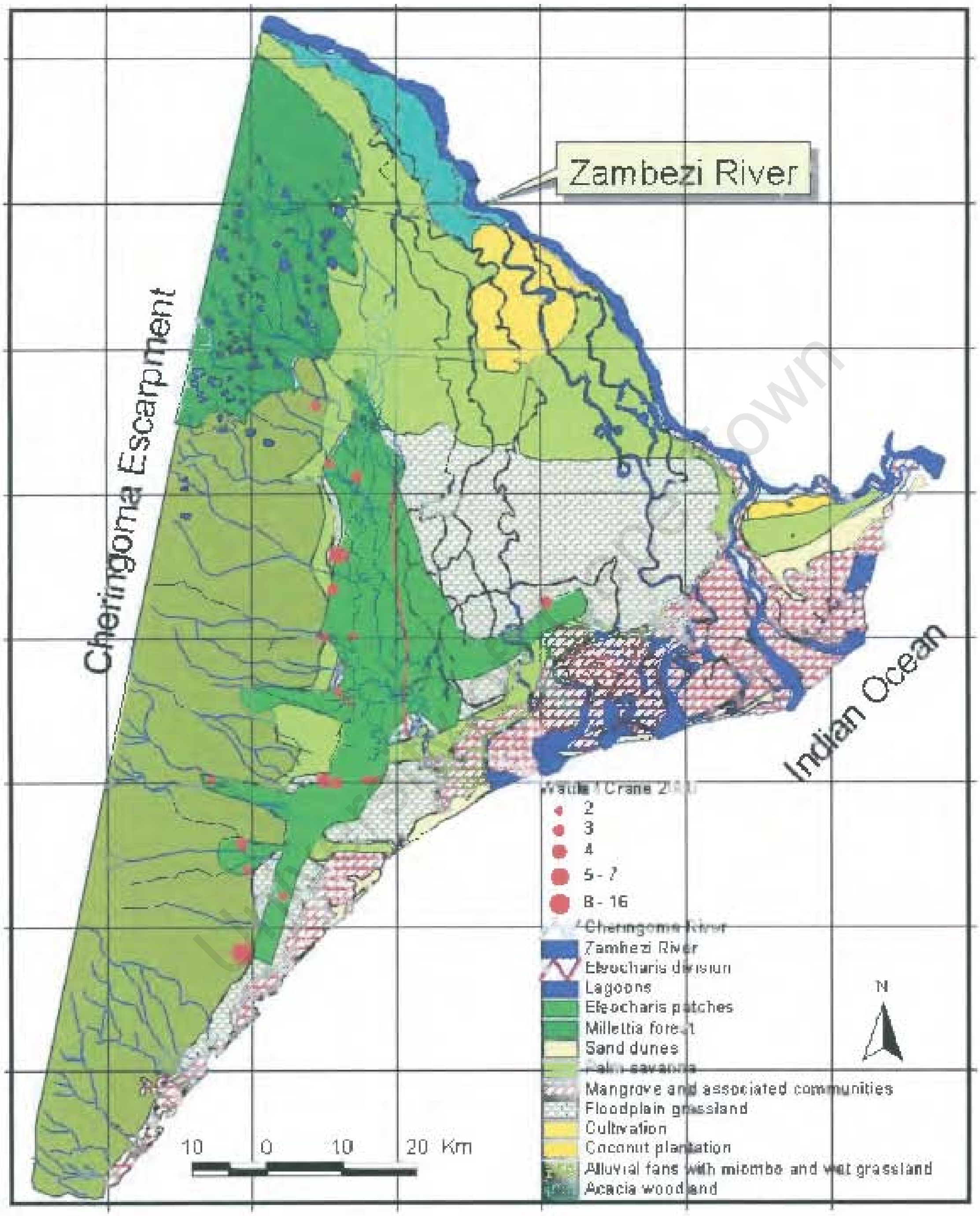
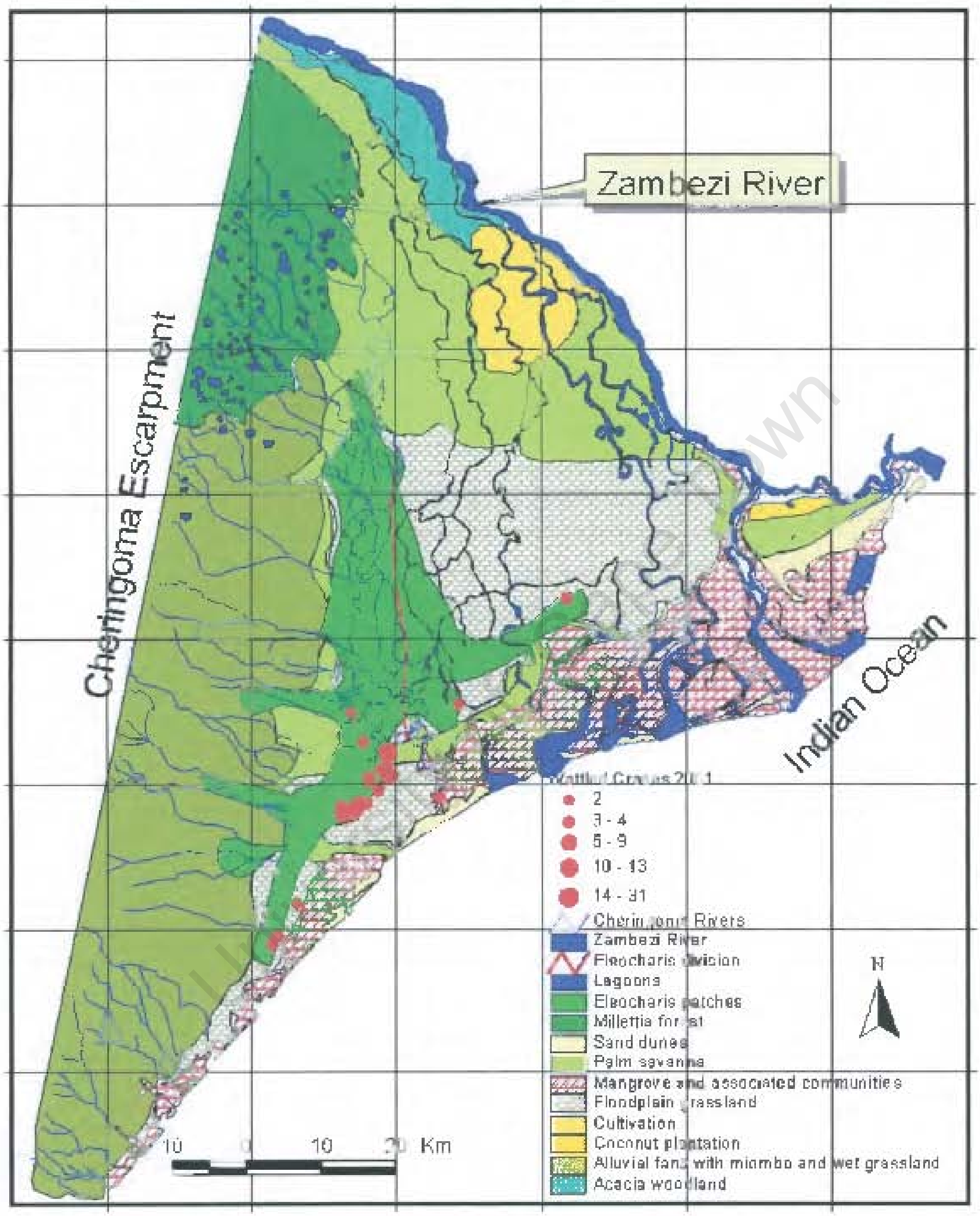


Figure 2. 3. The November 2000 Wattled Crane distribution.



In 2001, crane distribution across the Cheringoma *Eleocharis* beds changed again, with the birds being concentrated in the south and closer to the sea (Figure 2.4).

Figure 2.4. The November 2001 Wattled Crane distribution.



In terms of habitat, breeding Wattled Cranes were always associated with *Eleocharis* along small streams or at pans. During the dry season, several pairs were also observed foraging in areas of burnt *Eleocharis*. The occurrence of large foraging flocks of non-breeding Wattled Cranes on *Eleocharis* beds at the end of the dry season and early wet season emphasizes the importance of the *Eleocharis* habitat to cranes.

Based on the 1999, 2000 and 2001 surveys the total area of *Eleocharis* within the Delta is 900 km². This habitat can be divided into in two distinct portions. The beds located below the Cherigoma Plateau account for 650 Km², 72% of the total. Further east, in the area influenced by the Zambezi River, there are 250 km² of *Eleocharis* (28% of the total) (Figures 2.2 – 2.4). In the area influenced by Cheringoma Rivers, Wattled Crane densities were 0.12, 0.15 and 0.31 birds per km^2 in 1999, 2000 and 2001 respectively. The density in the area influenced by the Zambezi River was an order of magnitude less, peaking at 0.06 per km^2 in 1999 (Table 2.1).

The consistent difference in crane density between the Cheringoma and Zambezi areas indicates that, although *Eleocharis* is present in both areas, the carrying capacity of the sites influenced by the Cheringoma rivers is higher than that of sites influenced by the Zambezi (Table 2.1).

Population size and structure

Wet season surveys in 1995 and 1997 indicated little change in the number of pairs occupying territories (58 and 60, respectively, Table 2.2). No birds were seen in the wet season of 2001, when water levels were exceptionally high. Dry season (November) surveys between 1999 and 2001 showed a steady increase in the number of pairs on territories (from 12 to 41), paralleling a progressive increase in wet season rainfall during this period (Tables 2.2, 2.4). During the same period, observed chick production increased in absolute terms (from 5 to 11 chicks), but chick production per pair was higher in the dry year of 1999 than in the wetter years of 2000 and 2001. Numbers of non-breeding (flocking) birds showed no clear pattern, even when the flood year of 2001 was ignored. More birds were present in flocks in the wet season than in the dry season. At the end of the dry season, however, there was no relationship between the number of breeding pairs and the number of non-breeding birds in flocks. However, because, by definition, birds in flocks are aggregated, if one large flock was missed during surveys this would strongly influence both the data and their interpretation.

Table 2.1. Estimated numbers and density (birds/km²) of Wattled Cranes, including chicks, associated with *Eleocharis* during 1999, 2000 and 2001 aerial surveys.

SITES:	Cheringoma River Influence	Zambezi River Influence
AREA (km²):	650(72 %)	250 (28%)
1999 Birds:	79 (88%)	4 (12%)
Density/ km²:	0.12	0.02
2000 Birds:	97 (97%)	3 (3%)
Density/ km²:	0.15	0.01
2001 Birds:	203 (94%)	14 (6%)
Density/ km²:	0.31	0.06

Table 2.2. Summary of the seasonal counts of Wattled Cranes during aerial surveys.

	Wet Season			Dry Season		
Survey Date:	03/95	05/97	04/01	11/99	11/00	11/01
Coverage	50%	50%	50%	50%	60%	50%
Pairs on Territories:	58	60	0	12	25	41
Chicks:	0	0	0	5	6	11
Individuals in flocks:	40	59	0	25	7	31

There was a slight increase in the total number of cranes estimated to be on the Delta between 1995 and 1997 (Table 2.3). However, this difference was due mostly to an increase in the number of flocking birds. Given the errors associated with estimating numbers of non-breeders (flocking birds – see above), the difference - an increase of 9.9% - is probably insignificant.

Table 2.3. The number of pairs and unpaired individuals observed and estimated during the late wet season.

Date:	03/95	05/97	04/01
Observed number of pairs:	58	60	0
Estimated number of pairs:	116	120	0
Number of unpaired individuals:	40	59	0
Minimum total population:	272	299	0

Between 1999 and 2001, the number of pairs attempting to breed increased with increasing mean monthly wet season rainfall, from 24 pairs in 1999 to 82 pairs in 2001 (Table 2.4). Even in 2001, however, following massive flooding in the Delta, only 68% of the estimated pool of 120 pairs (based on surveys from 1995-1997) bred.

Table 2. 4. Wattled Crane population size in the late dry season of 1999-2001, together with estimates of their productivity and measures of rainfall.

SURVEY PERIOD:	11/99	11/00	11/01
Observed pairs:	12	25	41
Estimated of pairs:	24	42	82
Observed of unpaired:	25	7	31
Proportion of pairs attempting to breed*:	20 %	35 %	68 %
Estimated number of chicks:	10	10	22
Chicks per breeding pair:	0.42	0.24	0.27
Chicks per potential breeding pair:	0.08	0.08	0.18
Estimated total population, excluding chicks:	73	91	195
Monthly wet season rainfall (mm):	227.5	249.3	278.7
Monthly dry season rainfall (mm):	68.5	18	33.4

* Assuming the potential breeding population is 120 pairs (Table 2.3).

The increase from 24 to 42 breeding pairs between 1999 and 2000 occurred despite the fact that there was no overtopping of the Zambezi River in either year. The difference is due entirely to a greater number of birds breeding in the Cheringoma area.

The highest breeding success (0.42 chicks/pair; 1999) occurred in the year of lowest rainfall when fewest birds were breeding (Table 2.4). In the higher rainfall years of 2000 and 2001, breeding success ranged from 0.24 – 0.27 chicks/pair, averaging only 61% of the breeding success in 1999 (Table 2.4).

Discussion

The distribution of Wattled Cranes across the Zambezi Delta is highly non-random. In both wet and dry years they are almost exclusively associated with the sedge *Eleocharis*, which grows on the margins of streams and pans. This same association exists on the Kafue Flats (Douthwaite 1974), the Okavango Delta and elsewhere (Konrad 1981). The tubers of *Eleocharis* provide the main food supply for the cranes throughout their residence period. The main *Eleocharis* areas, and those supporting the highest density of Wattled Cranes, are found below the Cheringoma Plateau, where rivers and streams running onto the floodplain are unregulated. These wetlands experience some seasonal inundation in all years, conditions essential for the production of underground tubers, themselves the means by which *Eleocharis* survives the dry season (see Chapter 3). The occurrence of these seasonal inundations is not dependent on the overtopping of the Zambezi River. Additional patches of *Eleocharis* are found close to the coast: these occur on saline soils, a pattern not reported elsewhere. The reason for the existence of these patches appears to be the coincidence between peak river/stream flows and the equinoctial tides in March. High spring tides at this time prevent the flow of fresh water into the sea, causing it to backflood the floodplain. This annual inundation allows *Eleocharis* to complete its life cycle and, because of dry season water stress, promotes production of the tubers on which both it, and the cranes, depend. Some *Eleocharis* does occur in the higher reaches of the Delta: however these areas are permanently flooded and the *Eleocharis* consequently has very low tuber production (Chapter 3).

Between years, many pairs of Wattled Cranes appear to be territory faithful: alternatively, territories are repeatedly occupied, but by different birds. Within territories, however, the nest site selected varies from year to year, with birds moving away from the previous year's nesting site where, possibly, the *Eleocharis* resource base had been depleted. Rainfall, which affects flooding depth, also influences year-to-year territory occupancy. In dry years, pairs concentrate at the core of the seasonally flooded areas. In wetter years, the floodplain margins are used more extensively (Figures 2.2 - 2.4), presumably because core areas are too deeply inundated. In the wet years, the timing of breeding is more staggered than in dry years. Pairs occupy floodplain edge territories first and rear their chicks earlier than pairs using the core of the floodplain: the latter pairs can only take occupancy after flood levels have receded.

The increasing aridity of the Delta may have forced cranes to breed earlier than would have been the case historically, due to early burning. As a corollary, the smaller area of inundation may have decreased the carrying capacity of the Delta for cranes. There are many more territorial pairs present at the end of the wet season than are present at the end of the dry (breeding) season (Table 2.2 and 2.3). As early in the breeding season as May-June, many pairs abandon their breeding attempts and join flocks of other non/failed breeders. Many of these birds, in turn, move to the floodplain of the Savana River (B. Chande and R. Zolho, *pers. comm.*). Some pairs do attempt to breed in these secondary habitats, but with little or no success. That only a portion of the population should breed in any one year is not unusual. On the Kafue Flats, Zambia (also a hydrologically impacted region), in "normal" flood years, only about 40% of the population attempts breeding: in very dry years, this may decrease to as little as 3% (Douthwaite 1974).

Differences in crane density between the *Eleocharis* beds of the Cheringoma and Zambezi support the notion that the carrying capacity of the Delta for cranes has been reduced. There are two possible explanations for this difference. Firstly, Cheringoma is the preferred habitat and crane numbers are always at or close to carrying capacity. As a corollary, the very low numbers of the cranes on the Zambezi *Eleocharis* beds are simply a consequence of the source pool of birds being too small to occupy this area fully. Second, the low density on the Zambezi reflects the proportionally low carrying capacity of this area. Given that there are always "surplus" adults in the population, even in years when large numbers of pairs attempt to breed (Tables 2.2, 2.3), the second explanation is the most parsimonious. Whilst rainfall strongly influences the numbers of pairs attempting to breed at Cheriongoma (Table 2.4), it has little or no influence on the numbers attempting to breed on the Zambezi (Figures 2.2 – 2.4). The Zambezi *Eleocharis* beds no longer experience natural, annual inundation and it seems probable that tuber production in these beds is unable to support more than a handful of Wattled Crane pairs. If the life cycle of *Eleocharis* in this area has been severely affected, it seems unlikely that these beds will persist for long.

Based on relatively few aerial surveys, it is difficult to assess the existence or otherwise of population trends. In the late wet season of 1995 and 1997, the minimum population (excluding chicks) was 270-300 birds (Table 2.3). Numbers undoubtedly fall during the dry season because of seasonal emigration in response to falling water levels (Table 2.2). No within-year data are available to assess directly the extent of this decrease, but minimum numbers in the late dry seasons of 1999-2001 ranged from 49

(2000) to 113 (2001) (Table 2.2). This suggests that, on average, more than 50% of birds leave the Delta between March and November.

The number of birds, especially the number of breeding pairs, present on the Delta at the end of the dry season is strongly dependent (admittedly based on only three data points) on rainfall, increasing near-linearly with increasing rainfall (the implications of this for the species' population dynamics are explored in Chapter 4). In some years, however, it is likely that rainfall and crane numbers will be decoupled. For example, in the late 1980s and early 1990s much of sub-Saharan Africa experienced a prolonged drought (Olsson 1991, de Vries *et al.* 1997) that affected most of the key breeding sites for Wattled Cranes. One of the least affected areas was the coastal region of the Zambezi Delta. In the late dry season of 1990, 2570 Wattled Cranes were counted in the Delta, most of which were paired, suggesting that they had attempted to breed (Goodman 1992). There are no data on breeding success in this year, but it is certain that since 1995, numbers on the Delta have never approached this level. Surveys at the same time of year between 1999 and 2001 gave totals ranging from 1.9% to 4.4% of the 1990 total (Table 2.4). The 1990 figure can only be explained by a mass immigration event (from where is unknown); this figure does, however, suggest that the Zambezi Delta may act as a temporary refuge for cranes under conditions of extreme regional drought.

In years for which data exist, many pairs abandoned their breeding attempts early in the season (see above). Many of these birds left the floodplain, but it is unknown whether they attempted breeding elsewhere. The Kafue Flats are unlikely to provide alternative breeding opportunities because breeding on the Zambezi and Kafue systems is synchronized (Konrad 1981). The breeding season on the Okavango Delta starts approximately three months later than on the Zambezi (Konrad 1981) and it is possible that some displaced birds may attempt breeding here. Of those pairs that did remain to breed between 1999 and 2001, productivity ranged from 0.24 (2000) to 0.42 (1999) fledglings per pair per year. The implications of this variability and whether or not displaced pairs breed elsewhere are explored in Chapter 4. Although breeding population size was positively linked to rainfall, breeding success was not. Highest breeding success occurred in the driest of the three years; success in the other two years was 36-43% lower than in the dry year. These differences are not in any way linked to adult mortality, because they are based on ratios of surviving chicks to surviving pairs at the end of the breeding season. Thus, in higher rainfall years, mortality of eggs and/or chicks must have been higher than in the dry year of 1999. There are several possible explanations for this, none of which can be tested directly using the survey data. 1) Flooding is the proximal stimulus for breeding behavior and, based on the extent of inundation, many pairs establish territories in areas where the food supply (much of which would be inaccessible and invisible at the time of settlement) is marginal; 2) nests and chicks are more accessible to predators in wet years (intuitively, the opposite would be predicted, as is case with African Jacanas *Actophilornis africana* (Tarboton 2001)); and 3) Increased primary production during the wet years increases the fuel load and thus the extent and intensity of fires. Of the above possibilities, (1) and (3) are perhaps the most likely. In the case of (3) above, fires are suspected of being a significant cause of chick mortality. They are started for a variety of reasons, most of which (such as clearance of paths, providing access to water, and hunting bush meat) are likely to become more acute when vegetation is tall and dense (as would be the case following good rains). Because the floodplain water table overall is much lower than prior to the impoundment of Kariba and Cahora Bassa (Beifuss and Davies 1999), even following good rains the floodplain surface dries out much faster than it would have done in the past. Pre-impoundment, the floodplain was inundated for nine months of the year (Beifuss 2002) and most chicks would have fledged (and thus be able to escape fire) before the start of the main fire season. Today, fires can, and do, start almost throughout the year.

On the Kafue Flats, chick production per pair is maximal when the annual flood is of medium size (Douthwaite 1974). However, the number of pairs attempting to breed is proportional to the annual rainfall at both sites. This suggests that before changes to the hydrological regime of the Zambezi Delta, chick production might have followed a similar pattern to that observed at the Kafue Flats. If this is the case, the pattern of breeding on the Zambezi has changed and is no longer comparable to other wetlands in the region. The study of the Kafue Flats' Wattled Cranes was made before completion of the Itezhitezhi Dam, when the flooding regime was still natural and intact; it may have changed subsequently.

The abundance of large herbivores is likely to affect the frequency and extent of fire. In 1968 the combined numbers of buffalo, waterbuck, zebra, hippo and elefant were *ca* 61 100 (Tinley 1969). Aerial surveys conducted in the late 1990s estimated the herbivore population at less than 8 367 (DNFFB 1998). Grazers such as lechwe spp, zebras and wildebeest reduce the fuel load and hence the risk of fire. At the same time, their grazing action increases the accessibility of *Eleocharis* tubers to cranes. In other Wattled Crane areas, such as the Kafue Flats, Okavango Delta, Bengweulu Swamp and Luia Plain, Wattled Cranes and grazers occur in close association (Konrad 1981).

On the Zambezi Delta, the numbers of grazers have been reduced by *ca* 90% since the late 1960's (Beifuss and Bento 1998), mostly because of illegal hunting. In terms of making *Eleocharis* tubers available to cranes, fire has to some extent replaced the role of grazers in reducing above ground plant biomass. However, it appears that such benefits are offset, perhaps more than offset, by costs in the form of egg and chick loss to fire. Wattled Cranes at sites that still support healthy grazer populations have a higher breeding success (Kamweneshe and Beilfuss in press) than birds on the Zambezi.

Summary

Wattled Crane numbers in the Zambezi Delta appear to have decreased slightly since the mid 1990's, but fluctuate between years in response to rainfall. The birds are concentrated on *Eleocharis* beds below the Cheringoma Escarpment where patterns of seasonal water inundation have not been affected by upstream impoundments. Within this area, year-to-year changes in local distribution occur in response to flooding depth. Within the Cheringoma, there is an inverse relationship between the number of breeding pairs and individual breeding success. This suggests that there is a core area of optimal habitat within the Cheringoma and that in the wet years, additional pairs breed in response to an increased extent of flooding, but in habitats that are of poorer quality than the core area. Even in the wettest years, however, very few pairs attempt to breed on the remaining 250 km^2 of *Eleocharis* beds associated with the Zambezi River. These beds are no longer subject to an annual flooding regime, and all evidence points to their being unsuitable breeding habitat for cranes, presumably because of a lack of *Eleocharis* tubers.

Many pairs of cranes that establish territories in the wet season abandon them as flood levels recede. Failure rate is greater in dry years, although those birds that remain have a relatively high breeding success. Some failed breeders disperse locally and may attempt to breed again, but have low success. It is suspected, but not proven, that some failed breeders may disperse to the Okavango Delta.

Increasing aridity and a massive reduction in the grazer biomass on the floodplain has resulted in an increase in fire frequency. Fires now occur throughout the year whereas historically they only started after the breeding of Wattled Cranes was completed. The benefits that cranes derive from fire through increased access to underground food are offset by an increased mortality of eggs and young chicks as a result of fires. The medium to long-term effects of increased fire frequency on the persistence of the Cheringoma *Eleocharis* beds is unknown.

Chapter III: Habitat selection and use by Wattled Cranes

Contents

Introduction

Aerial surveys demonstrated that Wattled Crane distribution was closely linked to *Eleocharis* beds occurring along the base of the Cheringoma escarpment (Chapter II). However, such surveys provide little insight into how birds use the *Eleocharis* habitat or why, for example, they avoid *Eleocharis* beds associated with the Zambezi River. This latter observation in turn indicates that the presence of *Eleocharis* alone is inadequate to predict the presence of cranes.

An understanding of the factors and features that link *Eleocharis* and cranes can only be gained by direct observations of the behaviour of birds using this habitat and linking these observations to measurement of habitat parameters (e.g. Bibby *et al* 1992). This part of the study used ground-based observations of birds' behaviour and microhabitat parameters to answer two key questions:

- What abiotic (soil, water depth) and biotic (vegetation structure, food availability) factors influence the use of *Eleocharis* beds by cranes, and
- How do the cranes utilize these habitats on a seasonal basis?

Methods

An aerial survey of cranes in the Marromeu Complex was made in September 1998 to determine the positions of birds so that they could be relocated on the ground. This was followed up by the first ground survey in June 1999.

When cranes were located, they were approached slowly to within 500 m, using natural cover as camouflage, and the demographic make-up of the group was determined. After a 10-minute "acclimatization" period, focal animal observations were started, recording time spent foraging and feeding. Three components of this behaviour were recorded: time spent travelling to find food, digging for tubers and eating tubers. Time spent on other activities, such as preening, vigilance and roosting was also recorded and lumped as "other". Male and female time budgets were compared using chi-squared tests. Fourteen pairs were observed for an average of 1 hour per pair. When a group left the foraging area, environmental data were collected at the precise location where the birds had been active. Standing water depth was measured at 100 randomly located points within the foraging area, using a graduated rod. An index of soil penetrability was obtained by dropping a 30 cm length of sharpened steel wire from a height of 1 m at 100 randomly selected points and measuring the depth to which the wire sank in the soil. To measure vegetation cover, expressed as *Eleocharis* stems per m^2, five 1 x 1 m quadrats were placed on the ground and photographed. An additional five quadrats were photographed in an adjacent area of *Eleocharis* where the cranes were not seen to feed. To determine the relationship between stem density and tuber density, eleven quadrats were positioned within *Eleocharis* beds of differing stem density during the dry season. After recording stem density, the quadrats were dug up and all tubers were counted. Non-linear relationships between environmental variables were constructed using the "curve expert" software (ver. 1.35, Hyams 2001).

The annual *Eleocharis* cycle was determined from a series of 10 transects run from the river channel to the outer limit of *Eleocharis* occurrence on the floodplain in 1999. Each transect was located at different patch of *Eleocharis* along the floodplain. Along each transect a series of 1 x 1 m quadrats were positioned 2 m apart. Within each quadrat the following data were recorded: number of *Eleocharis* stems, number of underground tubers (calculated, see Figure 3.4), number of stems of other plant species, surface water depth or depth of the water table, and soil penetrability. Most of the associated plants were collected, labelled and pressed for identification at

Eduardo Mondlane University in Maputo. Water table depth was measured 5 hours after digging to allow the water level to stabilise. River depth was also measured in the centre of the river. The same transects were re-surveyed in subsequent years (using GPS references). Transects were made between the early dry season and early wet season along the edge of the Cheringoma floodplain. The eastern portion of the Cheringoma floodplain was only visited from early to late dry season, using an amphibious vehicle.

Relative insect density was recorded as the number of insects flushed by footsteps at the approximate position where cranes were feeding. A series of 10 transects was made, perpendicular to the river channel, each transect comprising 10 footsteps. Three people were involved in each transect. The person in front served to flush insects while the two behind counted insects flying off to either side of the lead person.

RESULTS

Crane foraging behaviour

Based on 807.5 minutes of observations of both males and females, there was little difference in the time spent travelling by the two sexes (Table 3.1). Females, however, spent approximately twice as much time digging for food and eating tubers than did males ($X^2 = 95.98$, d.f. = 3, $P<0.005$).

Table 3.1. Foraging time budgets (totals, in minutes) of male and female Wattled Cranes.

Activity	Males	Females
Travelling	108.9	106.2
Digging	25.9	78.9
Eating	135.1	263.7
Other	537.6	384.6
Total	807.5	807.5

Whilst *Eleocharis* tubers were the main food of both sexes, insects were also eaten in approximately equal numbers (an average of 1 insect.min^{-1}) by both sexes. The main insect prey was ground locusts whose abundance was greatest in dry and burnt areas (Table 3.2). Because of the reduced foraging time of males, they spent more time in "other" activities, most noticeably vigilance.

Table 3.2. Number of flying insects counted per footstep (S) on 10 transects (T) across the Delta floodplain during the dry season.

Steps	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10
S1	1	2	3	0	2	3	0	1	2	3
S2	1	0	2	3	3	0	3	2	0	2
S3	4	0	1	2	4	2	2	3	2	1
S4	3	3	0	1	3	6	5	5	3	6
S5	5	3	3	2	5	3	2	3	4	7
S6	3	4	2	4	4	4	4	2	5	4
S7	4	5	4	3	3	2	6	7	6	3
S8	5	2	3	6	2	6	4	5	2	2
S9	3	3	5	3	5	7	3	7	5	4
S10	3	2	2	1	8	4	4	8	6	3
Total:	32	24	25	25	39	37	33	43	35	35

Soil penetrability, water depth and habitats used by cranes

Areas in which Wattled Cranes fed were characterized by intermediate to high soil penetrability, with very few patches in which the soil was hard (Figure 3.1). Similarly, foraging areas were characterized by water depths of <550 mm (Figure 3.2). Once the water depth exceeds 550 mm, it becomes increasingly difficult for the cranes to dig for tubers. Water depth and soil penetrability are themselves closely and linearly correlated (Figure 3.3). That cranes are largely confined to soils of intermediate penetrability (Figure 3.1) is almost certainly a consequence of constraints imposed upon them by water depth (Figure 3.2): they are unable to feed in deep water, but also avoid completely dry areas where soil penetrability is very low.

Figure 3.1. Frequency distribution of soil penetrability measured at the exact positions used by feeding Wattled Cranes (r =0.93; S = 10.97; n = 997; P<0.001; S=standard error).

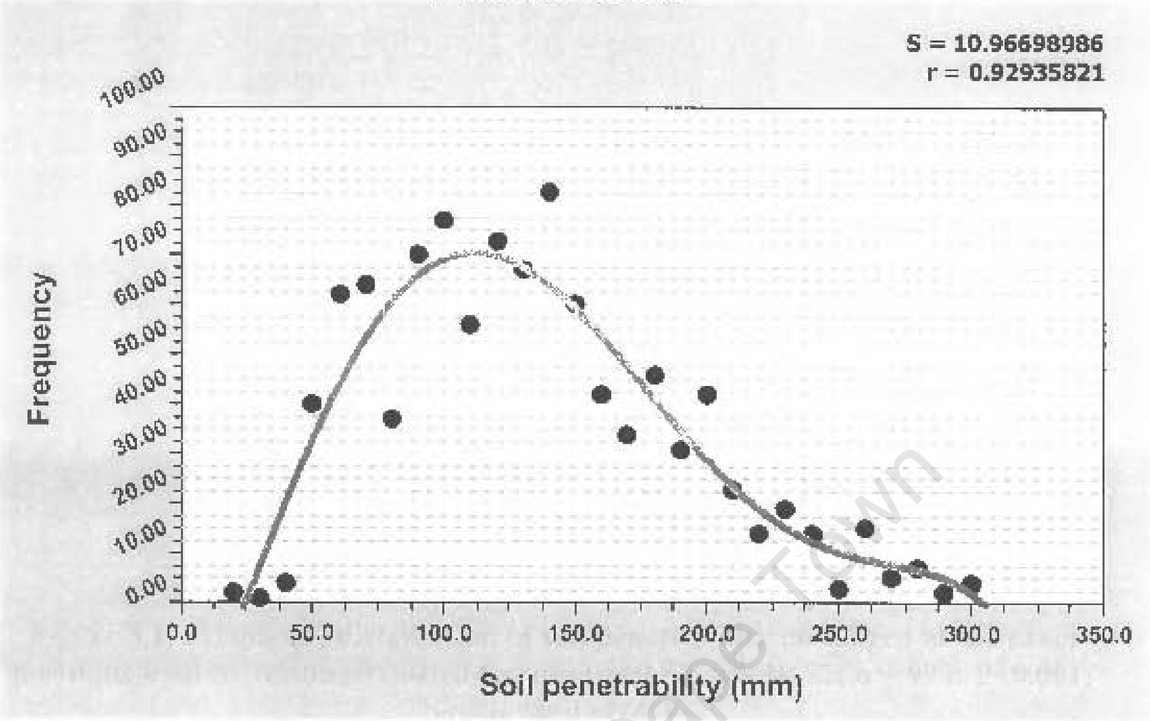
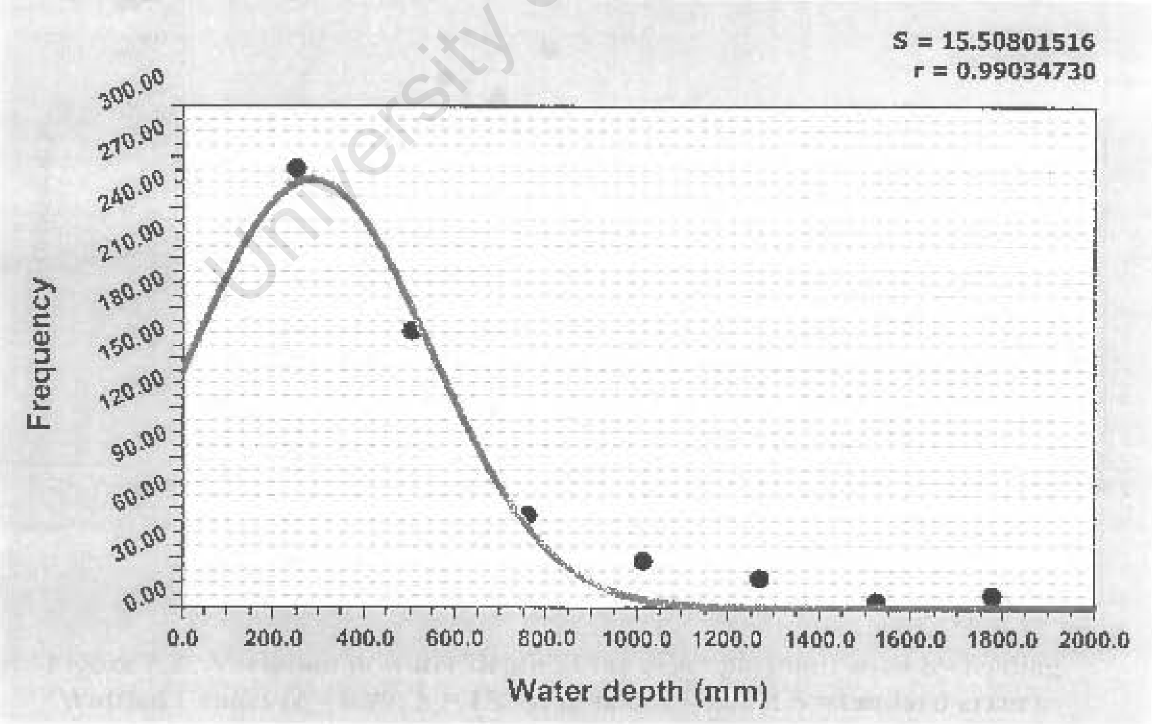
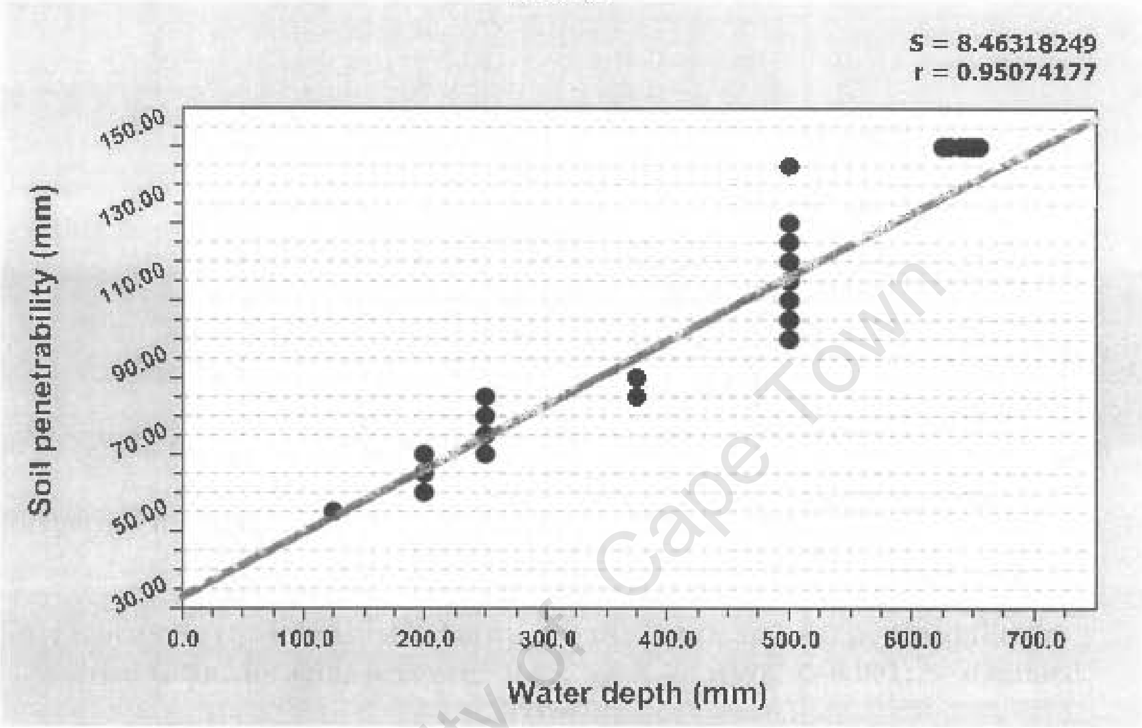


Figure 3.2 . Variation in water depth at the exact positions used by feeding Wattled Cranes (r = 0.99; S = 15.51; n=680; P<0.001; S=standard error).



However, the shallow water favoured by cranes also characterizes the edges of the Cheringoma floodplain, where *Eleocharis* beds are concentrated. Thus, it is difficult to be certain whether the cranes' avoidance of deeper water is a physical constraint on foraging or merely a response to the dispersion of food.

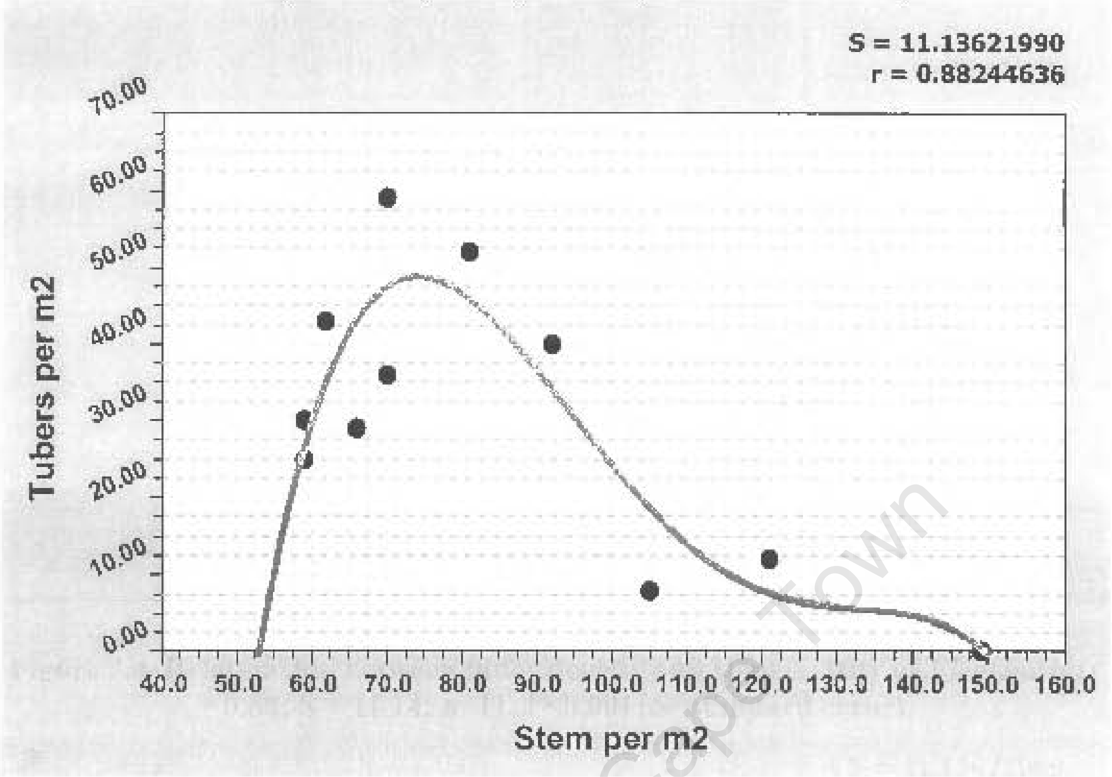
Figure 3.3. The relationship between water depth and soil penetrability in Wattled Crane foraging areas (r = 0.95; S = 8.46; n=98, P<0.001; S=standard error).



Eleocharis tuber density

The relationship between *Eleocharis* stem density (a measure of the above-ground productivity of the sedge) and tuber density (the productivity variable to which cranes respond) was strongly non-linear (Figure 3.4). Tuber density peaked between approximately 65 and 90 stems.m^{-2}; both above and below this stem density, tuber density decreased rapidly. Although the X-axis of Figure 3.4 is presented as stem density, it equally well represents a transect moving from a river channel out onto the floodplain. Thus, tuber density is maximal from close to the channels out to the mid floodplain, decreasing at the channel margin and on the outer floodplain. Figure 3.4 represents the situation at the end of the dry season in November when most of the floodplain is accessible to cranes.

Figure 3.4. Relationship between tuber density and stem density of *Eleocharis* (r = 0.88; S = 11.14; n=11, P<0.001; S=standard error).



The annual cycle of *Eleocharis* and the responses of Cranes

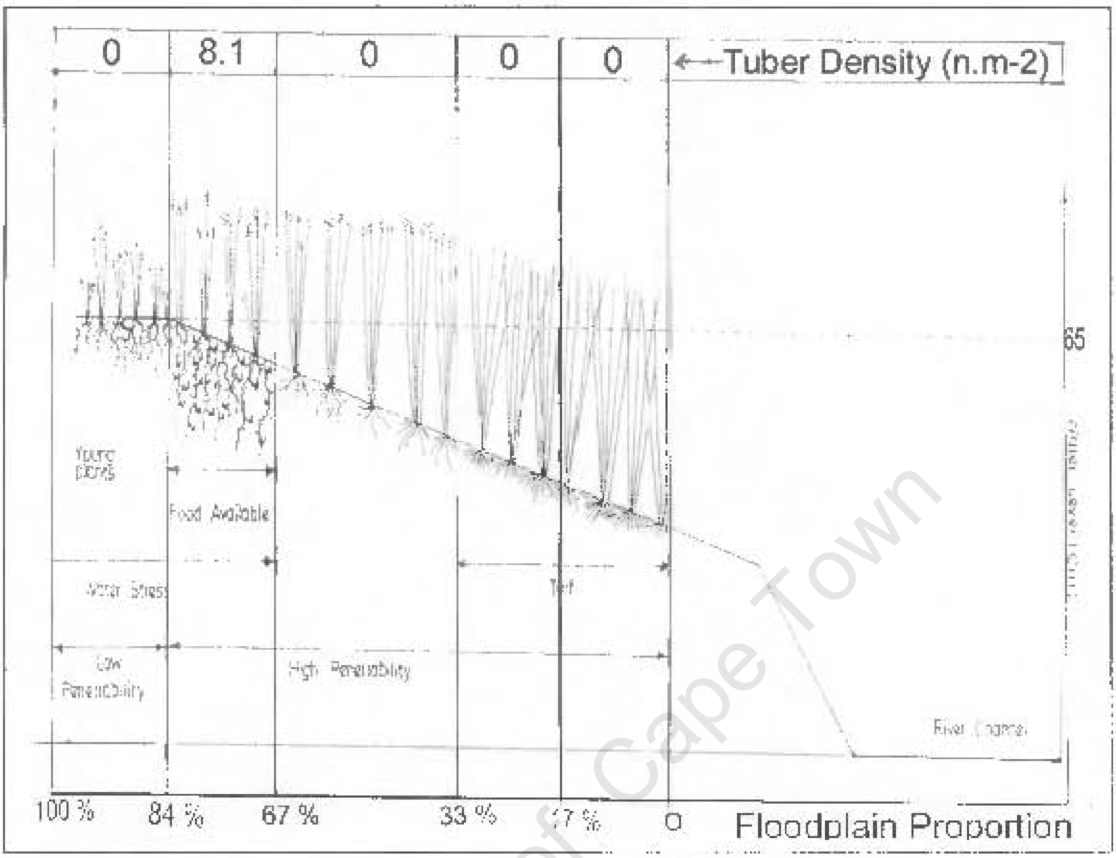
Growth, reproduction and tuber production of *Eleocharis* are strongly influenced by the flooding regime. Tubers are produced by mature plants in response to water stress (as a mean of storing water) (Lavery and Blackman 1969, Blakers *et al* 1984) and it can thus be predicted that the distribution of tuber-producing plants on the floodplain will change seasonally. Below I describe this seasonal variation by means of a series of schematic diagrams, starting in the early dry season at the end of the summer rains. These diagrams illustrate cross-sections of the floodplain, referenced to the position of a river channel and associated water level. Areas of high and low soil penetrability are indicated, along with zones of water stress and tuber availability.

The early dry season (May - July)

As water levels start to recede at the end of the rains, three different "strategies" are evident among *Eleocharis*, resulting in a clear zonation of tuber and non tuber-producing plants (Figure 3.5). At the outer edges of the floodplain, young plants that have become established during the rainy season occur at high densities. These plants avoid desiccation by a combination of high stem density and the fact that they are mostly covered by several layers of dead plant material. The effect of this "matting" is to create a sponge-like matrix that is efficient at trapping and retaining atmospheric water in the form of dew, fog and rain. These plants do not produce tubers. Closer to the channel margins, *Eleocharis* stem density is lower and other sedge species are interspersed in the matrix. These communities do not have the spongy structure of the outer *Eleocharis* beds and are exposed to increasing desiccation stress as the dry season progresses, in response to which they produce tubers.

At this time, the tuber-producing zone of the Cheringoma floodplain accounts for approximately 17% of its total area and has an average tuber density of >8 tubers.m^{-2} (8 tubers.m^{-2} measured after cranes had foraged in the area). At this time of the year, most cranes fed singly or in pairs, were highly territorial and chased intruders away from their foraging areas. No flocks of cranes were seen on the floodplain in the early dry season, although a flock of 29 birds, mostly juveniles and immatures, was located on the floodplain of the nearby Savana River.

Figure 3.5. Profile diagram of *Eleocharis* beds in the early dry season (May - July).

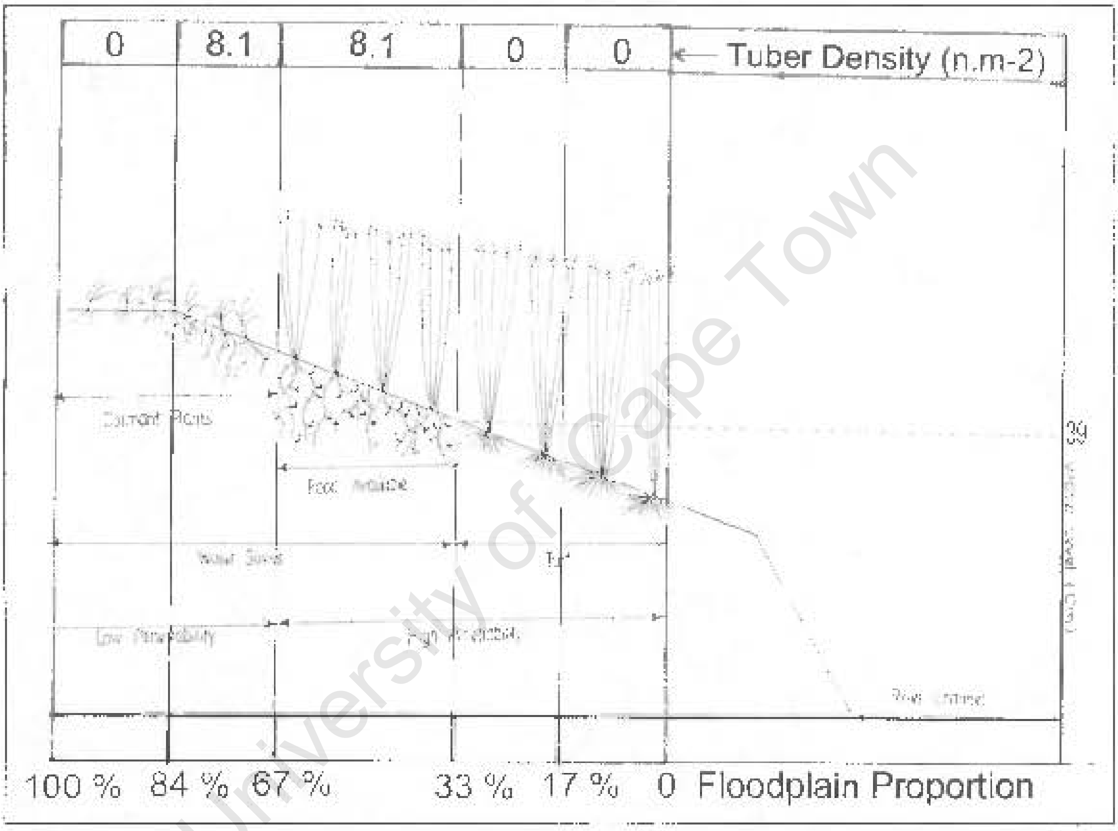


The mid dry season (August – October)

As water levels continue to fall, young plants on the outer floodplain – which is now completely dry – become dormant, but do not produce tubers. These plants, which are of no value to Wattled Cranes, cover approximately 17% of the entire floodplain. At the same time the zone of water stress closer to the river channels expands to cover about 65% of the floodplain. However, most of the tuber-producing plants that were exploited by cranes early in dry season have now become unavailable because the increasing desiccation has reduced soil penetrability and hence compromised the birds' ability to dig up the tubers. As a result, about 35% of the floodplain is now available to foraging cranes (Figure 3.6). As in the early dry season, tuber density in these areas measured after cranes had fed there was 8 tubers.m^{-2}.

This is the season in which young Wattled Cranes hatch. At the same time, flocks of 4-6 "floaters" were regularly seen, as was a flock of 25-29 juvenile and immature birds, assumed to be the flock that was located on the Savana River floodplain early in the dry season.

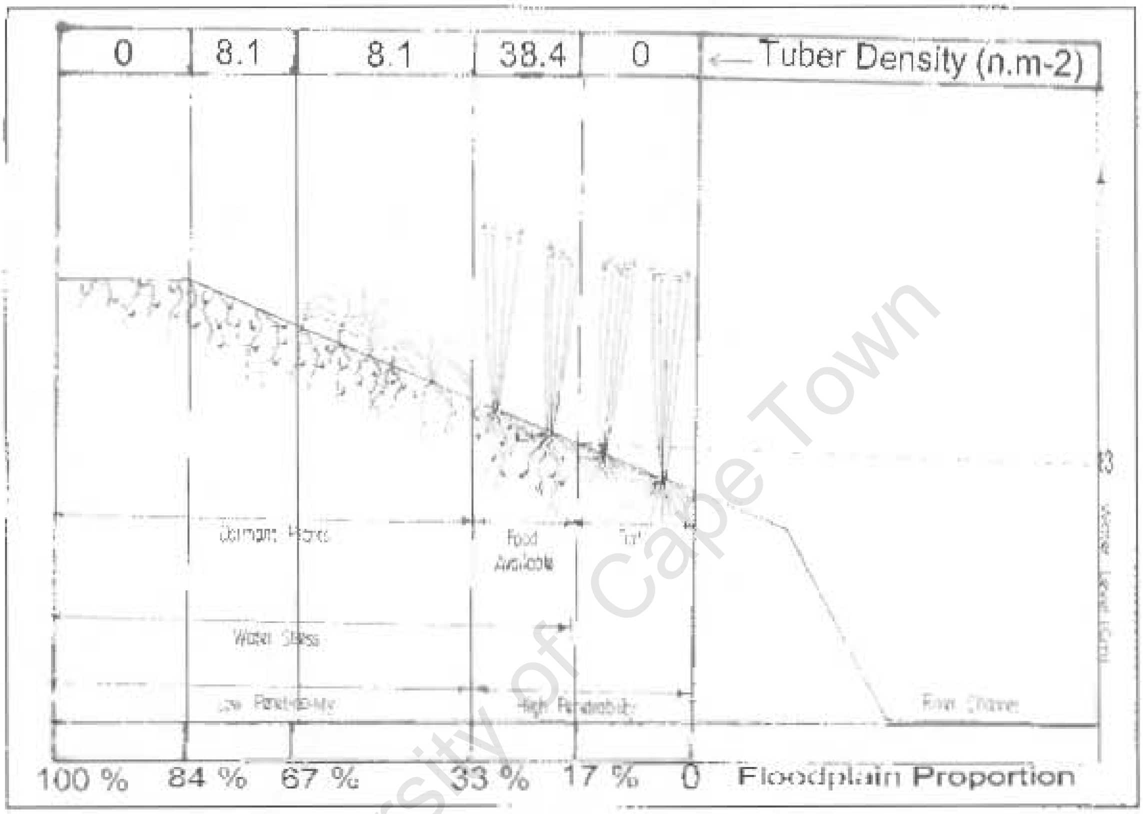
Figure 3.6. Profile diagram of *Eleocharis* beds in the middle of the dry season (August – October).



The late dry season (November)

By this time, more than 85% of the Cheringoma floodplain is dry. Dormant *Eleocharis* plants cover 70% of the floodplain and the proportion of the area where soil penetrability is high enough to allow cranes to forage decreases concomitantly. In total, about 85% of the floodplain is under water stress and the area available to cranes has decreased to 15% of the total; the remaining 15% close to the channels is permanently flooded and the plants here produce no tubers (Figure 3.7). Although the area available to foraging cranes is at its lowest point of the dry season, tuber density is relatively high, averaging 38 $tubers.m^{-2}$.

Figure 3.7. Profile diagram of *Eleocharis* beds at the end of the dry season (November).



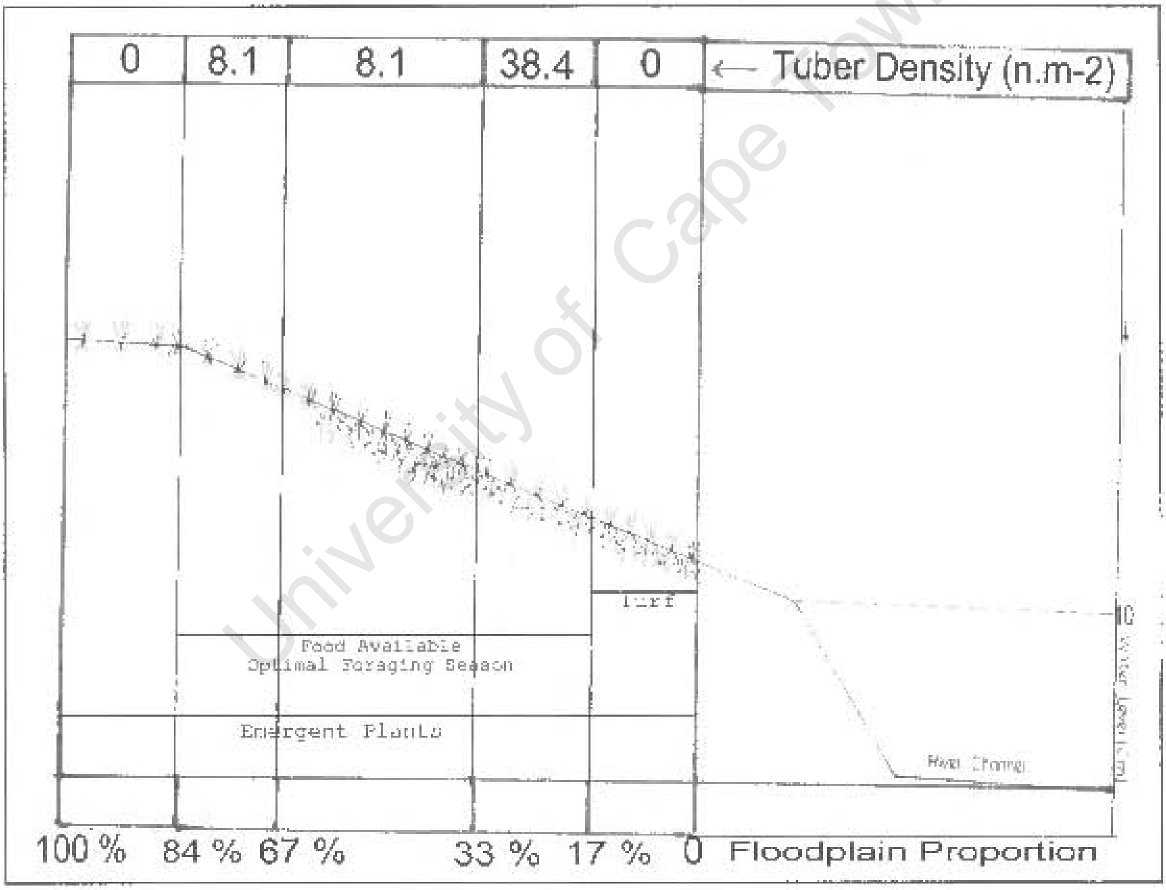
This period of high tuber density coincides with the fledging period of Wattled Cranes when the energy demands of family groups are at their highest. Family groups sometimes coalesce into flocks of 5-7 birds and the flocks of "floaters" can become as large as 60.

Although tuber density is high at this time of the year, the plants producing tubers are also very tall, making it more difficult for cranes to access the tubers. It is also the time of the year at which fire frequency is highest: much of the Delta is burned, including many areas of tuber-producing *Eleocharis*. Burning improves accessibility of the tubers to cranes, and many birds foraged on burnt areas at this time. Burning also provides additional food sources in the form of insects and small mammals that have been killed by the fires.

The early wet season (December-January)

At this time of year the floodplain receives the first significant rain it has experienced for 7-8 months.

Figure 3.8. Profile diagram of *Eleocharis* beds early in the wet season (November-January)



Within three days of the first rainfall, the entire floodplain is covered in *Eleocharis* shoots. At the same time, the tuber-bearing plants that were inaccessible to cranes because of low soil penetrability now become available and cranes can forage over

70% of the floodplain. Tuber density ranges from 8-38 tubers.m^{-2}, providing the best foraging conditions of the year for Wattled Cranes (Figure 3.8).

At this time, family units from the preceding dry season remain cohesive and on their territories: much space is therefore available for additional birds. Many "new" pairs arrive on the floodplain and attempt to establish territories. At the same time, large foraging flocks of 60-100 birds form.

The mid wet season (February - March)

By this time the river channels and associated pans are full of water but generally have not overtopped onto the floodplain. The entire floodplain is covered in short- to medium-height grasses and sedges. In addition to *Eleocharis*, the sward includes *Echinocloa* sp., *Acroceras* sp., *Oryza* sp., *Paspalum* sp., and *Leersia hexandra* (Beilfuss *et al* 2000, Beifuss 2002), most of which are seed-producing species. The generally damp conditions promote the germination of *Eleocharis* tubers, but these are of low nutritional value to cranes. At this time cranes spend most of their time grazing on the grass sward. The frequency of courtship behaviour increases and many of the "new" pairs that arrived on the floodplain at the beginning of the wet season have now established territories. Egg-laying takes place after a large flood event, normally in mid- to late March. Floater flocks are still present and the total Wattled Crane population of the Delta peaks at this time.

End of the wet season (April)

This is the wettest time of the year and the entire floodplain is inundated with water. Because there is no water stress, there are no *Eleocharis* tubers available for cranes, but nonetheless large numbers of cranes remain on the Delta. Most of the grasses associated with *Eleocharis* beds are seeding at this time and a high seed biomass persists for about 4-5 weeks and forms the primary food source for the cranes. As water levels start to recede at the start of the dry season, seed availability decreases, as does the carrying capacity of the Delta for cranes. Many cranes leave the Delta at this time: the normal pattern is for the floaters (that are frequently involved in interactions with territory-holders) to leave first, followed by pairs occupying poor quality territories. As water levels recede further, *Eleocharis* tubers gradually develop and occur across about 15% of the *Eleocharis* beds by the early dry season (mid-May).

DISCUSSION

Crane foraging behaviour

During the breeding season, time-activity budgets indicate that food (energy) intake by females is considerably greater than that of males, which spend more time in vigilance behaviour (Table 3.1). The greater energy intake of females may be related both to the costs of egg-formation and of incubation. Typically of cranes, both sexes incubate by day, but night-time incubation, when ambient temperatures are lower, is undertaken entirely by the female (Meine & Archibald 1996).

The high vigilance level of males during the breeding season is almost certainly a response to predation risk. Wattled Cranes reacted strongly to the presence of Serval Cats *Felis serval*, flying as far as 1500m when disturbed (*pers. obs.*). Similarly, prolonged periods of aerial vigilance were directed at Martial Eagles *Polemaetus bellicosus* circling high overhead. They were equally wary of people, showing changes in behaviour at a range of about 1000m and usually did not allow an approach closer than 700-900m before walking or flying away.

Although it is possible that Serval Cats could prey on adult cranes, it seems likely that vigilance is primarily aimed at chick protection. Even when capable of flight, chicks rarely stray more than two metres from their parents and both adults are highly vigilant: the same pattern has been observed for Whooping Cranes (Howe 1989). When a family group flies off in response to predation threat, the chick is bracketed (one ahead and one behind) by the adults (pers. obs.).

It is unknown how the time-activity budgets differ between wet and dry seasons: all observations were made during the dry season because of the inaccessibility of the floodplain at other times. Courtship and nest building undoubtedly become time-consuming activities, and pairs were observed dancing in January (early wet season).

Habitat use

The macro-scale distribution of cranes on the floodplain is determined (for most of the year) by the distribution of tuber-bearing beds of *Eleocharis*. Tuber formation is linked to water stress and thus to water depth. As water levels fall, tuber production increases, but the penetrability of the soil decreases, making it increasingly difficult for cranes to dig up the tubers (Figures 3.1, 3.2, 3.3). Most cranes forage in water depths of <600mm, but they are also capable of foraging in areas lacking surface water providing the water table is not more than 250mm below the surface (pers. obs.). This value was obtained from several excavations and water table measurements.

Because extremes of aridity and inundation create conditions unsuitable for crane foraging, the birds' distribution on the floodplain tracks seasonal changes in water levels and follows seasonal production of *Eleocharis* tubers.

Responses of cranes to the annual cycle of *Eleocharis*

In broad terms, the floodplain area can be divided into three zones. The channel margins remain wet for the longest (to all intents and purposes they are flooded throughout the year), and the outer floodplain is the last to be inundated and the first to dry out. The area between these extremes, termed the intermezzo, experiences regular seasonal flooding and drying.

It could be predicted that *Eleocharis* would respond to the apparent gradient of increasing water stress from the channel margins to the outer floodplain by increasing tuber production along the same gradient; this is not the case. In the permanently inundated channel margins, there is no water stress and no tuber production and these areas are not used by foraging cranes. Reproduction by *Eleocharis* in this zone is exclusively sexual.

On the outer floodplain, *Eleocharis* plants are small, densely and thickly leaved, and accumulate many dead leaves. This matrix traps atmospheric moisture and, during the dry season, rather than producing tubers, these plants become dormant. Their failure to produce tubers may be a result of water limitation, even during the wet season. The high densities of *Eleocharis* on the outer floodplain exclude most grass species, seed bearing grasses only becoming abundant between the outer limits of the *Eleocharis* beds and the miombo woodland at the foot of the escarpment. Most, perhaps all, *Eleocharis* plants on the outer floodplain are seedlings, probably resulting from sexual reproduction of channel and intermezzo plants.

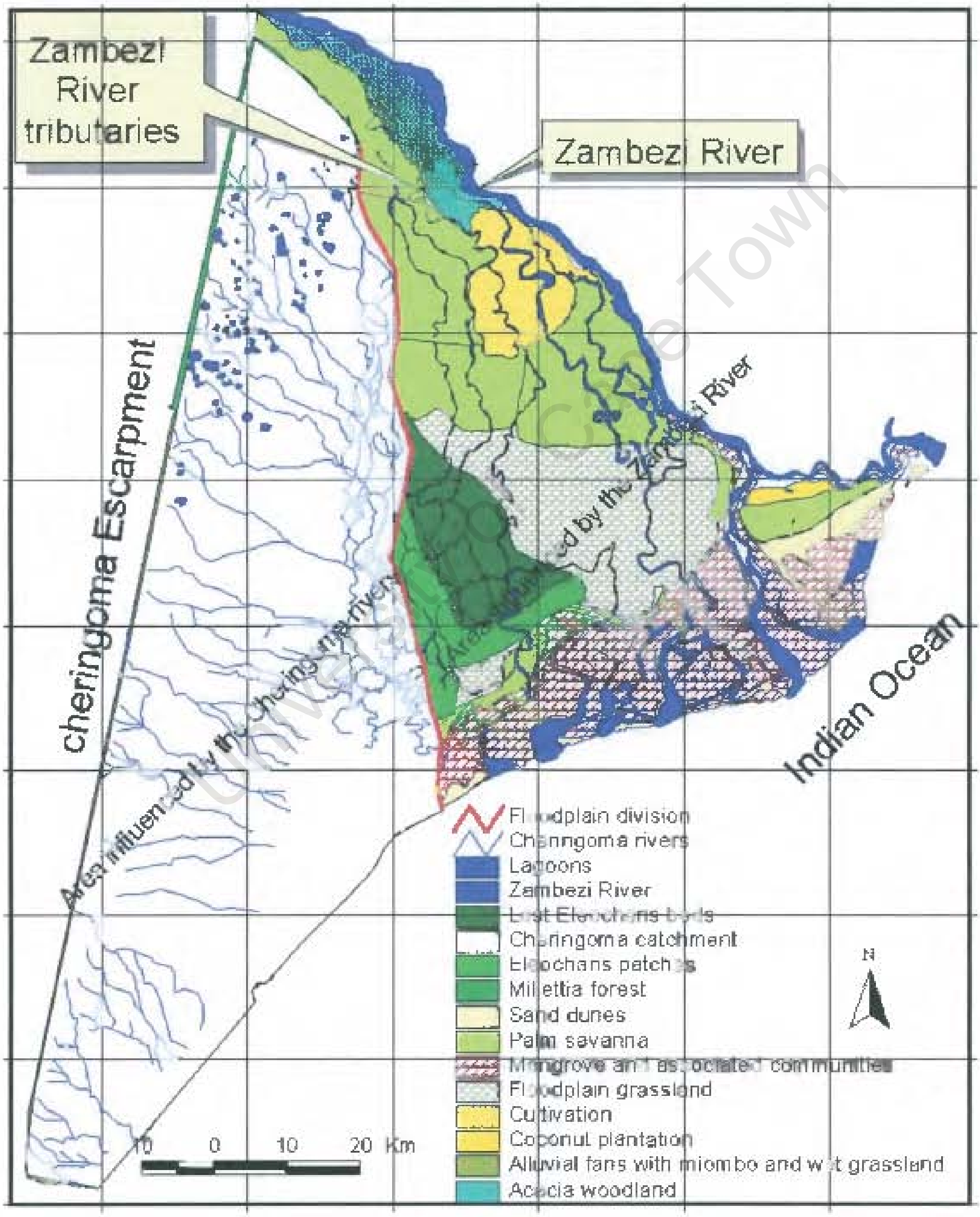
The *Eleocharis* plants of the intermezzos show the greatest response to water stress in terms of tuber production. Plant density is lower than on the outer floodplain and several seed-bearing grass species co-occur with *Eleocharis*. The *Eleocharis* plants on the intermezzos reproduce both sexually and vegetatively and provide tubers for Wattled Cranes in all but the wettest time of year (when grasses and their seeds become important foods).

Similar patterns in the growth and reproduction of *Eleocharis* have been recorded in other southern African wetlands, including Zambia's Kafue Flats (Douthwaite 1974, Konrad 1981) and on Australian river floodplains where the tubers are the major food of Brolgas (Lavery and Blackman 1969, Blakers *et al* 1984) and Magpie Geese *Anseranas semipalmata* (Frith & Davies 1961).

Zonal differences in the annual cycle of *Eleocharis* on the Cheringoma floodplain (natural flooding regime) explain why the remaining *Eleocharis* beds associated with Zambezi River are not utilised by Wattled Cranes. The sites where *Eleocharis* occurs on the Zambezi are either permanently inundated (equivalent to the Cheringoma channel margins) or are at the extreme outer limits of the floodplain, equivalent to the small plants on the outer floodplain of the Cheringoma: in neither situation are tubers produced. *Eleocharis* has disappeared from the intermezzo areas of the Zambezi because of prolonged drought associated with upstream impoundments. Comparing the present zonal distribution of *Eleocharis* associated with the Cheringoma to the remnant *Eleocharis* beds of the Zambezi, it seems likely that the area of *Eleocharis* on the Zambezi has been reduced by about 50% (Figure 3.9). This is based on the historical distribution of river channels. Only one pair of cranes breeds on the Zambezi *Eleocharis*, suggesting that there is only one tiny portion that continues to function "normally". The degradation of the site under the Zambezi is directly related to the lack of water from the Zambezi River (Figure 3.9) and is indirectly affected by the absence of natural siltation (Suschka and Napika 1986, Beifuss and Davies 1999). The natural siltation processes which provide nutrients for wetland plants only happen on the Cheringoma floodplain (Beilfuss *et al*

2000). Poor nutrient supplies elsewhere result in low plant productivity (Bunting and Elston 1966, Guime and Curtis 1976, Sykora 1979).

Figure 3.9. Distribution of good runoff conditions from the Cheringoma rivers and the drought areas associated with Zambezi River tributaries. The dark green areas indicate where *Eleocharis* beds under the influence of the Zambezi River are assumed to have been lost.



Although *Eleocharis* is clearly vital to the Delta's Wattled Cranes for much of the year, and especially during the breeding season, peak crane numbers occur in the wet season when grass and grass seeds form much of the diet. As water levels recede and *Eleocharis* again dominates the diet, crane numbers decrease. Not only do the floaters leave the Delta, but so do many pairs that had attempted to establish breeding territories. The combination of a decreasing foraging area and the presence of territorial pairs probably explains the transience of floaters. What is less easy to explain is the departure of many territorial pairs (it is unknown whether these birds achieve breeding opportunities elsewhere). The proportion of territorial pairs that remains appears to be influenced by the extent of summer flooding: more pairs remain in wet years but, on average, achieve a lower per pair chick production than occurs in dry years (Chapter II). This strongly suggests that in most, perhaps all, years, the number of pairs attempting to breed on the Delta exceeds the area's carrying capacity. There are two possible explanations for this: as yet, these cannot be distinguished because of lack of knowledge of the species' site fidelity. Firstly, Wattled Cranes exhibit low site fidelity and the regional (southern African) population of birds exceeds carrying capacity such that birds displaced from elsewhere attempt to breed on the Delta. Secondly, Wattled Cranes exhibit high site fidelity (and are long-lived) and the present apparent surplus of potential breeders is a legacy of a time when the carrying capacity of the Delta was higher (i.e. before the degradation and loss of the Zambezi *Eleocharis* beds).

Summary

Crane foraging behaviour

During the breeding season food intake by females is greater than that of males. This is presumably a response to higher energy demands of females during the incubation period. Males spend more time in vigilance behaviour in response to predation risk, especially the risk of predation to the chicks.

Habitat use

The distribution of adult Wattled Cranes is determined by the occurrence of underground tubers and foraging areas are characterized by intermediate to high soil penetrability and water depth <600 mm. These parameters are closely correlated and cranes avoid dry areas where penetrability is low, because of the difficulties in extracting tubers. Distribution on the floodplain changes seasonally in response to water depth and tuber production by *Eleocharis*.

The annual cycle of *Eleocharis* and responses by cranes

Eleocharis tuber production is strongly influenced by the flooding regime. As the water level recedes early in the dry season the outer edge of the floodplain dries out and 35% of the floodplain is exposed. Although the exposed area experiences water stress, only 17% of the total floodplain area (in the intermezzo area) produces tubers.

During the middle of the dry season, approximately 65% of the floodplain is under water stress. However, many of the tuber-producing plants exploited by cranes early in the dry season are no longer available because of low soil penetrability. Around 35% of the floodplain is available to foraging cranes and it is at this time that Wattled Crane chicks hatch.

By the late dry season more than 85% of the floodplain is dry and under water stress. About 70% of the *Eleocharis* beds are unavailable to foraging cranes. In addition, another 15% of the floodplain close to the channels is permanently flooded and lacks tubers. On the remaining 15% of the floodplain, however, tuber density is high. This period of concentrated food coincides with the fledging period when the energy demands of the family groups are highest. At this time burning becomes important in increasing tuber availability by reducing above ground plant biomass improving tuber accessibility. When foraging on burnt areas, cranes eat both insects and small mammals as well as tubers.

Within a few days of the first summer rains the entire floodplain is covered by *Eleocharis* shoots and more then 70% of the floodplain is available to cranes foraging on tubers. Family units from the preceding dry season remain cohesive on their territories. Thus, much space is available for additional birds to establish territories.

By the mid wet season, in addition to *Eleocharis*, numerous grasses and other sedges are available on the floodplain. Most of these grasses are seed producers, diversifying the foraging options for cranes. At this time courtship behaviour is frequent, more pairs establish territories and the Wattled Crane population peaks.

By the end of the wet season the entire floodplain is inundated with water and tuber production is low. Grass seed biomass is high and forms the primary food source for the cranes. However, after 4-5 weeks, seed biomass decreases, as does the carrying capacity of the Delta for cranes. Many cranes leave the Delta. The floater flocks are the first to leave follow by pairs occupying poor quality territories. As the dry season progresses tuber production gradually increases.

Chapter IV: Simulation modelling of the Zambezi Delta Wattled Crane population.

Contents

Introduction

Changes to the hydrology of the Zambezi Delta have almost certainly impacted Wattled Cranes, especially in those parts of the Delta directly influenced by flooding of the Zambezi River (Chapter III). However, observations of numbers of cranes and their breeding performance over relatively few years (1995-2001) are, in themselves, insufficient to evaluate the long-term consequences of these changes.

Despite the short time span of the database, it is clear that rainfall plays a major role in the cranes' population dynamics, influencing not only the number of breeding pairs on the Delta, but also their productivity. For this reason, a model driven primarily by rainfall was deemed appropriate as a means of assessing likely long-term population trends. A key objective for constructing such a model was to assess whether Wattled Cranes would persist in the Delta in the absence of significant intervention in the form of water management. This obviously is vital in determining the need for (costly) monitoring and management. Specifically, this part of the study had three objectives:

1. To determine likely trends in the Wattled Crane population of the Zambezi Delta in the absence of further hydrological management (i.e. to determine population viability given the *status quo*);
2. To compare scenarios under which a) there is no production of chicks in the Zambezi (eastern) portion of the Delta, and b) there is no chick production by the Cheringoma population (i.e. conditions in this area become unsuitable for breeding).
3. Assess the level of management required (or not) to maintain a viable population of Wattled Cranes on the Delta.

Methods

Models were constructed using rainfall as the driving variable. The Wattled Crane population can be broadly divided into two sectors, those breeding on the Cheringoma floodplain and those on the Zambezi floodplain. Both sectors respond positively to wet season rainfall in terms of the number of pairs attempting to breed (Figures 4.1, 4.2).

Figure 4.1. Relationship between monthly wet season rainfall and number of crane pairs attempting to breed on the Cheringoma floodplain (r =1; S = 0).

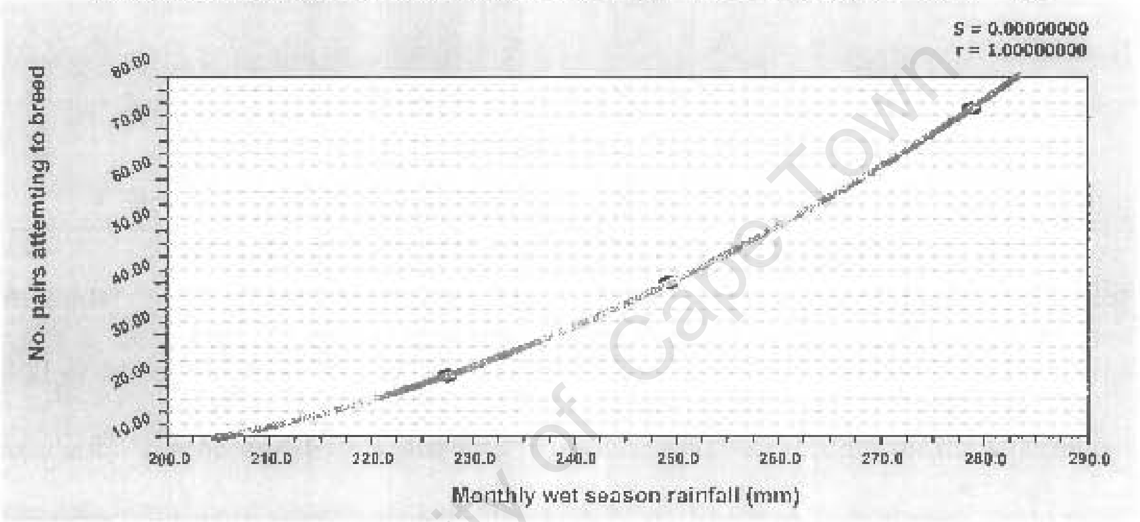
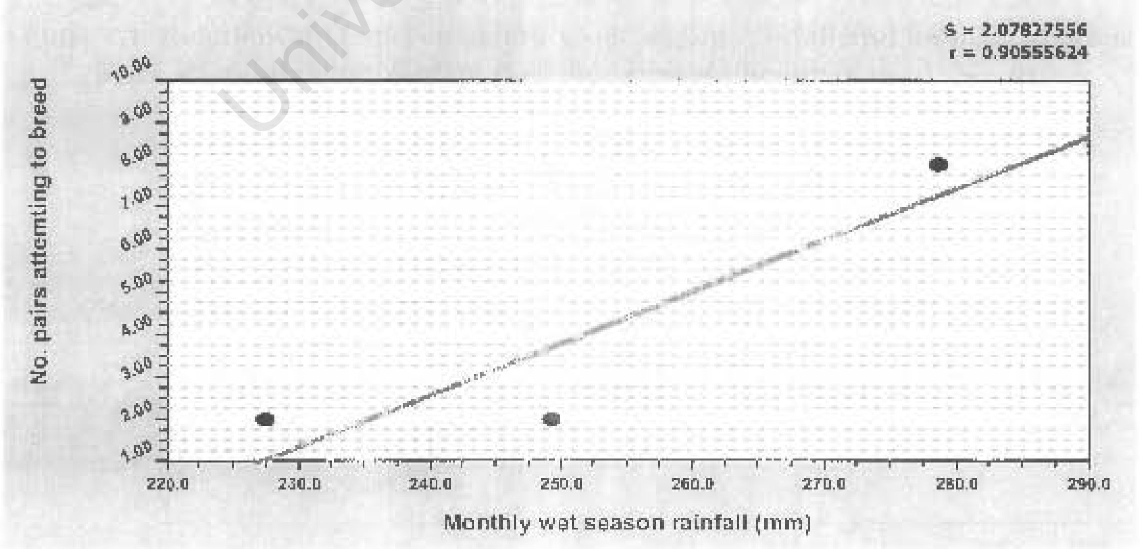


Figure 4.2. Relationship between monthly wet season rainfall and number of crane pairs attempting to breed on the Zambezi floodplain (r = 0.91; S =2.08).



In terms of productivity, however, the two sectors respond differently to dry season rainfall. On the Cheringoma, productivity is highest in wetter years (Figure 4.3), but on the Zambezi, it is maximal in dry years (Figure 4.4).

Figure 4.3. Relationship between monthly dry season rainfall and chicks per breeding pair on the Cheringoma floodplain (r =1; S = 0).

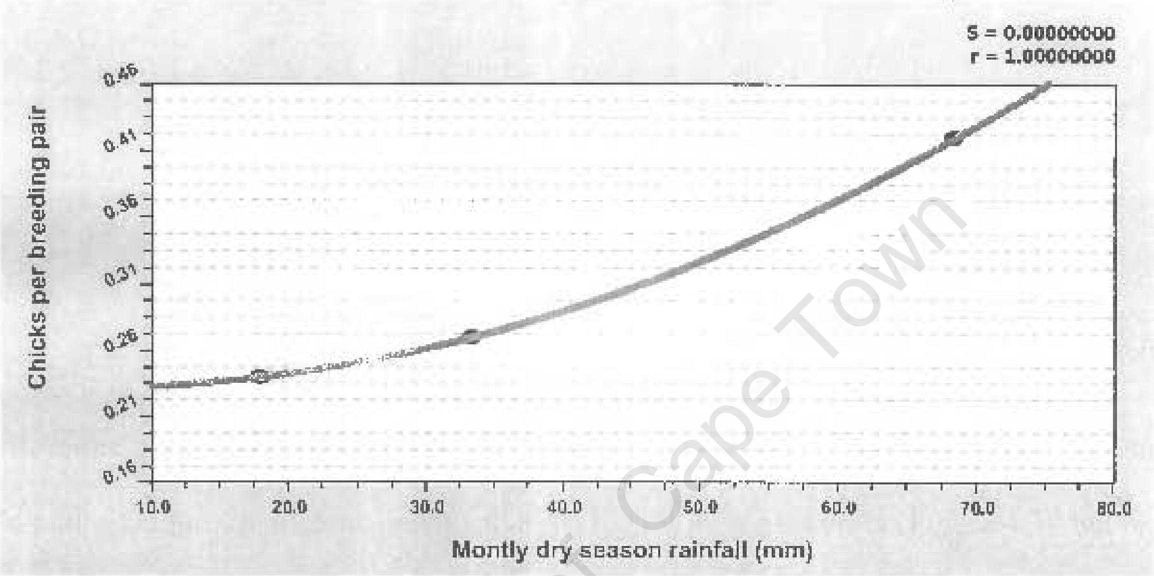
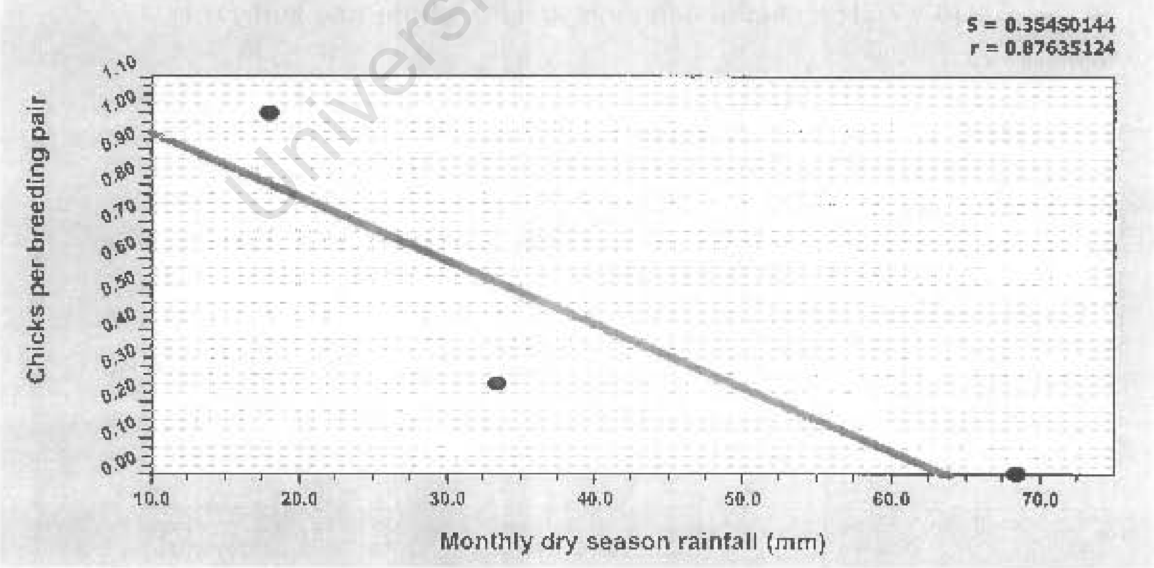


Figure 4.4. Relationship between monthly dry season rainfall and chicks per breeding pair on the Zambezi floodplain (r = 0.88; S = 0.36).



Wattled Crane numbers are far higher on the Cheringoma than on the Zambezi floodplain (Chapter II). For this reason, a simple simulation model was developed for the entire Delta using "average" relationships between rainfall, breeding numbers and productivity. In a second set of simulations, the Cheringoma and Zambezi were modelled separately, driven by site-specific regressions of population parameters on rainfall (Figures 4.5). This enabled more detailed comparison of the contribution made by each sector to the total population.

Models were built using Stella Research Software 5.1.1 (HPS 1996). The crane stock was divided into two components - "breeders" and non-breeding "mature" birds (= floaters) – apportioned on the basis of rainfall (regression equations from Figures 4.1-2). Mature birds were defined as being more than five years old. Because of a lack of knowledge about Wattled Crane movements in Southern Africa, the worst-case scenario was modelled in which there was no immigration into the Delta.

Population size (assuming no immigration or emigration) is a function of birth and death rates. Whilst birth rate could be empirically incorporated into the model, no data exist on survival rates of Wattled Cranes in the Delta. In South Africa, annual mortality rate of adult Wattled Cranes is 6% (based on a Population and Habitat Viability Analysis – McCann *et al* 2000). However, a substantial proportion of this mortality results from collisions with power lines and from poisoning. Neither of these factors is operative on the Delta, and the annual mortality rate of breeding adults was assumed to be 3%. Mortality rates of chicks were assumed equal to those of Whooping Cranes *Grus americana* (Boyce 1987, Kuyt and Goossen 1987, Mirande *et al* 1997). Mortality rate in the first year was 9%, decreasing by 1% annually. Mortality rate in the sixth year is thus

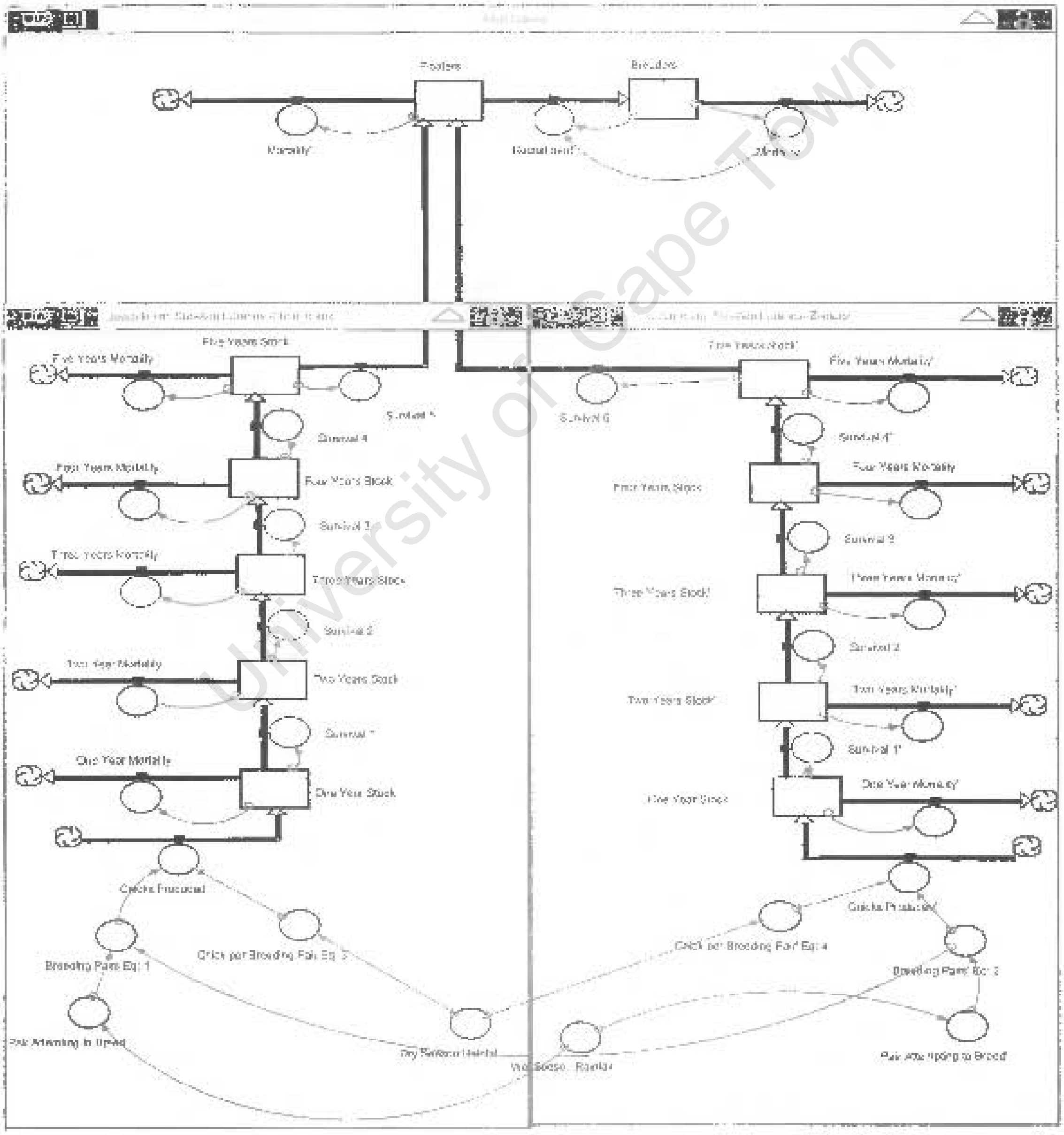
4%. This value of 4% was also applied to members of the floater population >5 years old, based on the assumption that the mortality rate of mature floaters (which, by definition, are mobile and opportunistic) is slightly higher than that of territorial breeders.

Wet and dry season rainfalls, expressed as mm per month, were entered as separate variables in the models. Values were randomly generated, but constrained both to have a normal distribution and to fall within the ranges experienced on the Delta since the completion of the Cahora Bassa Dam in 1974. The modelled rainfall distribution was not significantly different from normality (wet season rainfall: $X^2 = 12.6$, d.f. = 10, P=0.75; dry season rainfall: $X^2 = 12.6$, d.f. = 10; P=0.75; Appendix (4) I).

Flow diagrams summarizing the models' structures are presented in Figures 4.5. Rectangles indicate stocks of breeders floater, and birds <6 years old. Circles indicate rates, defined by simple equations (Appendix 4 II)) and bold lines indicate transitions from one state to another. The end points of all bold lines indicate death. All models generated two key outputs on an annual basis: size of the breeding population, and size of the floater population.

The model started with a stock of 240 breeders. The initial number of breeders was based on the maximum number of pairs observed on territories during the wet season (n=120, Chapter II). In Table 4.1 the initial number of one-year-old chicks (n=10, Chapter II) was based on the minimum number of fledged chicks observed at the Cheringoma and Zambezi sites combined (Table 4.1) in years of normal rainfall conditions (Chapter II). Numbers of two-year-old and older chicks were based on first year chick numbers and a mortality rate of 9%, decreasing by 1% annually. The juvenile stock was not included in the floater population. Before members of one stock are passed along to the next stock, the total is rounded off to the nearest whole number. Number of floaters was determined as 300 (maximum total numbers on Delta - Chapter II) minus 45 (number of 1-5 years birds based on 10 first-year birds and numbers of 2-5 years birds calculated from mortality rates) minus 240 (maximum number of breeding birds; Chapter II).

Figure 4. 5. Model comparing Wattled Crane productivity between the Cheringoma and Zambezi floodplains.



The number of breeders at the Cheringoma Site is obtained from the total number of breeders into the Delta (n=240, Chapter II) minus the maximum numbers of breeders at the Zambezi Site (n=14, Chapter II).

Table 4.1. Initial stock values used in the Wattled Crane population simulation model.

Scenario:	Current population	Cheringoma	Zambezi
STOCKS	Whole Delta	Cheringoma	Zambezi
Breeders	240	226	14
Floaters	15	14	1
1 year stock	11	10	1
2 years stock	10	9	1
3 years stock	9	8	1
4 years stock	8	7	1
5 years stock	7	6	1
Total:	300	280	20

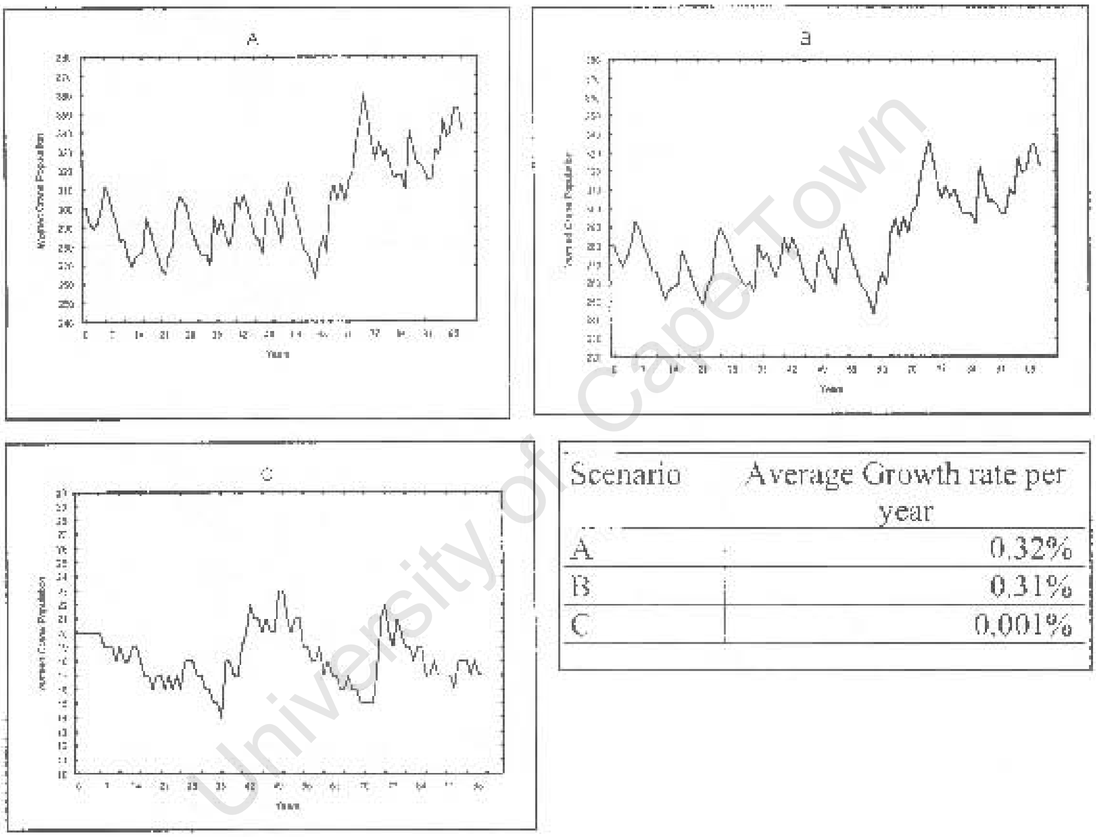
Three model simulations and one sensitivity test were made. The first scenario models trends in the total Wattled Crane population of the Delta over the next 100 years for the baseline conditions described above. The second scenario models these trends for Cheringoma population alone (i.e. assuming loss of the Zambezi population). Scenario three models the future of the Zambezi population alone, assuming loss of the Cheringoma birds. The sensitivity of the model to elevated mortality rates of breeding adults (4 -7%) was assessed.

Results

The first scenario (current baseline conditions) predicts an average population growth rate of 0.32 % per year (Fig, 4.6a). Should the Zambezi floodplain population be lost (scenario two), the Wattled Crane population is still self-sustaining with slightly lower growth rate of 0.31 % per year (Figure 4.6b). If there is no contribution from pairs breeding on the Cheringoma floodplain, the population is self-sustaining (growth rate of

0.001% per years), but with very small numbers, potentially at risk from stochastic events (Figure 4.6c).

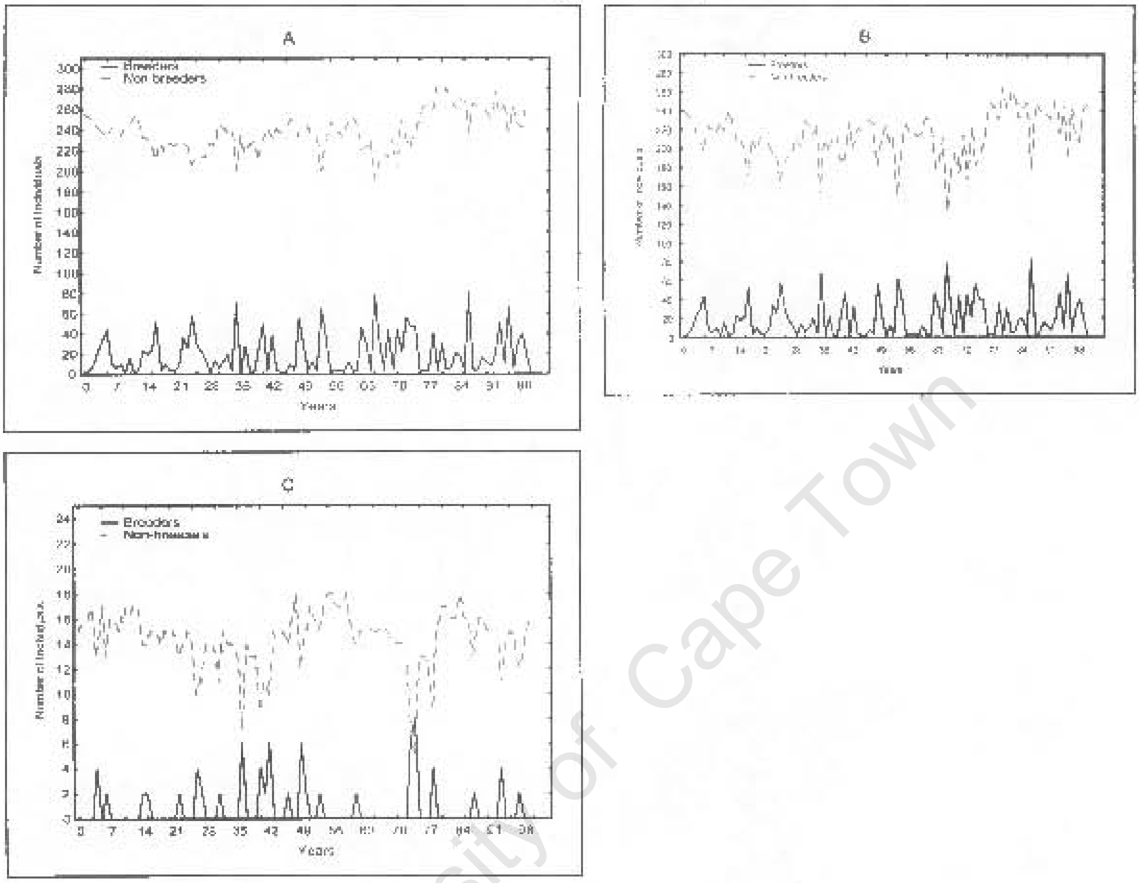
Figures 4.6. Wattled Crane population trends including breeding adults, floaters and juveniles/immatures <6 years old, assuming (a) no changes to the *status quo*, (b) zero productivity on the Zambezi Floodplain and emigration of the Zambezi birds (*status quo* on the Cheringoma), and (c) zero productivity on the Cheringoma Floodplain and emigration of Cheringoma birds (*status quo* on the Zambezi Floodplain).



Scenario	Average Growth rate per year
A	0.32%
B	0.31%
C	0.001%

The number of breeding adults fluctuates annually, with new breeders recruiting from the floater population during high rainfall years and the reverse occurring during years of low rainfall (Figure 4.7). If the *status quo* persists (Figure 4.7a), or if only Cheringoma birds are present (Figure 4.7b), the number of non-breeding adults always exceeds the number of breeders at the end of dry season. If the Zambezi population alone remained, there would be many years in which no birds bred (Figure 4.7c).

Figures 4.7. Numbers of breeding birds and mature floaters by the end of dry season under scenarios of (a) The *status quo*, (b) loss of Zambezi birds, and (c) loss of Cheringoma birds



Similarly, loss of this population would have a very small effect on total chick production in the Delta (Figures 4.8a-c).

Because the Cheringoma and Zambezi population respond differently to dry season rainfall (Figures 4.3, 4.4), numbers of chicks produced annually by the two populations are not closely synchronized (Figure 4.9).

The Wattled Crane population model is very sensitive to changes in the mortality rate of breeding adults. Although the population growth continues to be positive up to a mortality rate of 5 %, an increase to 6% mortality results in a decreasing population (Table 4.2).

Figure 4.8. The number of fledged chicks present in the Delta if (a) the *status quo* persists, (b) if only Cheringoma birds bred successfully, and (c) if only Zambezi birds bred successfully.

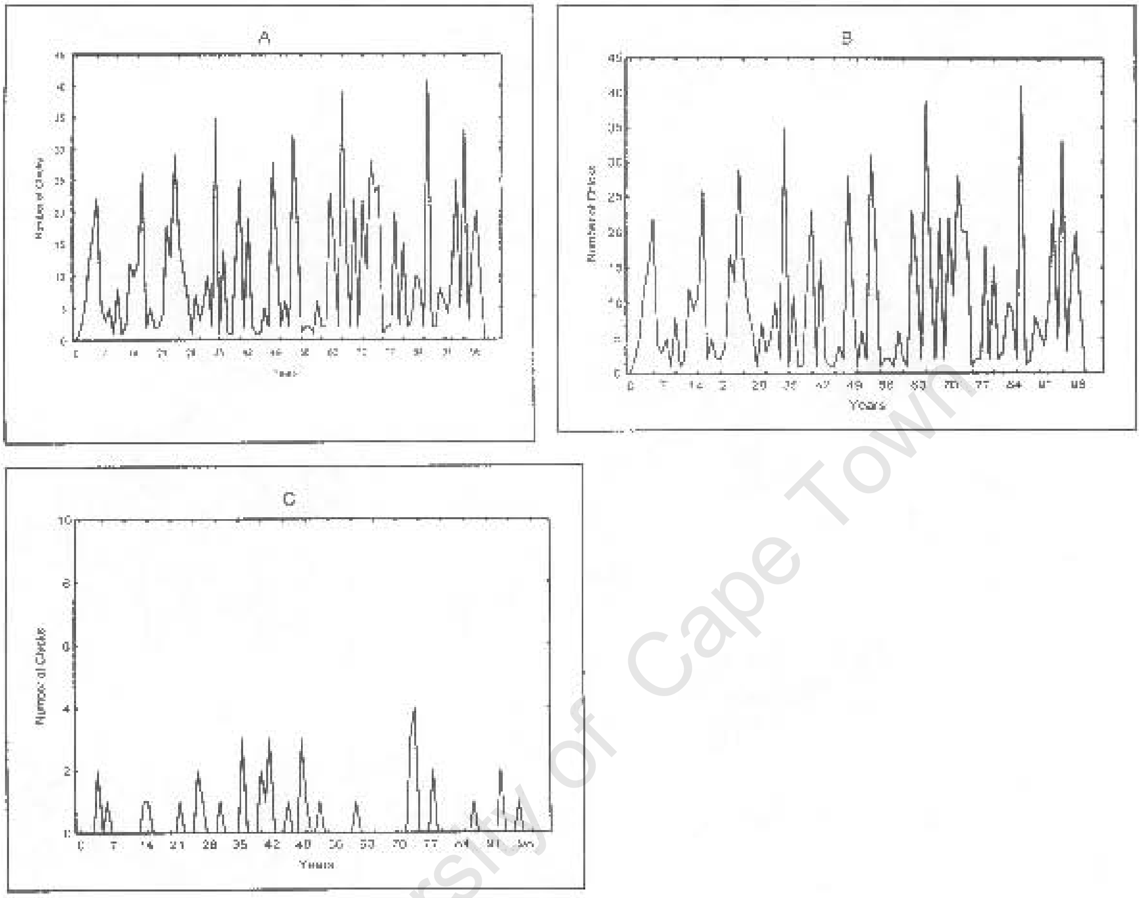


Figure 4.9. Simulation showing lack of synchrony in breeding performance between the Cheringoma and Zambezi crane populations.

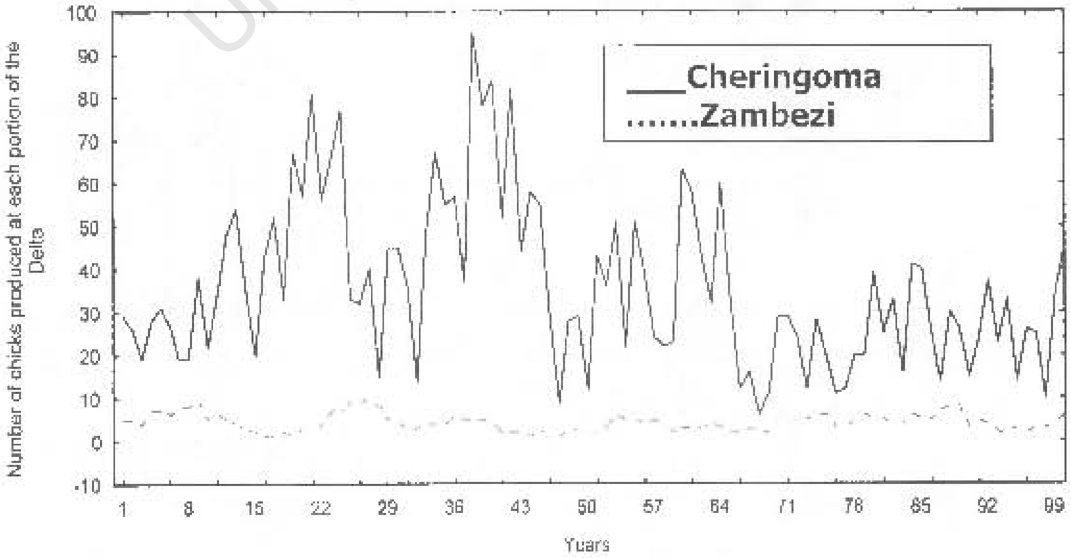


Table 4.2. Population responses of the Marromeu Wattled Crane population to different rates of breeding adult mortality.

Mortality rate	Population growth rate per year	Population trend
3%	0.32	++
4%	0.12	+
5%	0.10	+
6%	-0.24	- -
7%	0.43	- - -

Discussion

The model suggests that the present population of Wattled Cranes in the Zambezi Delta is viable despite the long-term, severe hydrological degradation of large parts of the floodplain. Under current conditions, the population is growing at a rate of 0.32 per year (Figure 4.6a). Even if conditions worsen on the Zambezi floodplain and only Cheringoma breeding pairs contribute to the population, the Wattled Crane population will continue to be self-sustaining at growth rate of 0.31 per year and is predicted to recover from the loss of Zambezi birds (Figure 4.6b). However, under this scenario, the Delta's productivity is slightly lower. Although the Delta's population growth rates under scenarios I and II differ slightly, the average number of chicks produced annually differs significantly ($t=4.64$; $p<0.05$; $N=101$) (Figure 4.8a, mean=10, S.D.=9.9; Figure 4.8b, mean=9.5, S.D.=9.8).

Should conditions worsen on the Zambezi Floodplain, the Cheringoma population will not only increase but, assuming a carrying capacity of about 300 birds, will at times export birds to other systems (Figure 4.6b). Although models (scenario III) predict the Zambezi population to be stable, its very low numbers (Figure 4.6c) would make this population vulnerable to catastrophic events.

Although the Delta's Wattled Cranes are currently self-sustaining, results do highlight the importance of efforts to increase the carrying capacity of the Zambezi sector of the Delta. At present, the long-term sustainability of the Wattled Crane population is entirely dependent on the maintenance of suitable breeding conditions on the Cheringoma floodplain and, metaphorically, all the birds' eggs are in one basket. Any activities that threaten the Cheringoma directly (e.g. development of rice agriculture on the floodplain) or alter the hydrological balance of the Cheringoma (e.g. replacement of natural miombo vegetation with *Eucalyptus* plantations) may seriously threaten the Wattled Crane population. Such threats are real: the human population is increasing rapidly on the Cheringoma escarpment, and, in 1998, the timber company Mondi Corporation proposed a large *Eucalyptus* scheme on the escarpment within the catchment of the Cheringoma rivers.

All suitable habitats below the Cheringoma escarpment appear to be saturated with breeding pairs and there is thus little opportunity for the Delta population to increase in the future (Chapter 3). Further, because the birds are spatially restricted, they are vulnerable to catastrophic events, such as tropical cyclones. The Zambezi Delta is frequently affected by major tropical storms, with an average of 5.6 strikes per decade since 1950, and these have resulted in significant damage to the Delta's estuary (Beilfuss *et al* 2002). Meine and Archibald (1996) note that small crane populations are particularly vulnerable to natural disasters. The population of Whooping Cranes in Lousianna (now extirpated) was reduced by more than 50% after a single hurricane in 1940 (Meine and Archibald 1996).

The sensitivity analysis indicates that the Delta's Wattled Crane population is potentially risk from factors that increase the mortality rate of breeding adults. If the mortality rate reached the same level (6%) as occurs in South Africa (McCann *et al* 2000), then the Delta population will experience a negative growth rate and decrease to less than 30 breeding pairs within 30 years (Table 4.2). The mortality rate in South Africa is almost certainly higher than in the Delta, because the Delta has relatively few powerlines (one of the major sources of adult mortality in South Africa). However, the mortality rate of breeding adults could increase due to effects of local poverty in the Delta (especially hunting with dogs) and chick mortality may increase because of the increase in grassland fires (Chapter 3).

The global population of Wattled Cranes appears to be decreasing (Chapter 1) and the potential production of surplus adults in the Marromeu could play an important role in sustaining populations elsewhere in southern Africa. The irruption of more than 2500 Wattled Cranes, mostly in pairs, to the Zambezi Delta in the early 1990s (Goodman 1992) suggests that there is substantial movement and exchange of breeding adult birds among southern African wetlands - such numbers could only have been sourced from one of the large wetland systems in Zambia or Botswana (Chapter 2). If the carrying capacity of the Zambezi floodplain could be increased to 35 pairs through improved hydrological management, the Delta population could become a major source of surplus adults for the region. Such an increase in carrying capacity may not be unreasonable. Several comparably sized wetland systems in Southern Africa support substantially larger numbers of breeding pairs than the Zambezi Delta, including the Kafue Flats (Konrad 1981, Kamweneshe and Beilfuss in press) and Bangweulu Swamps in Zambia

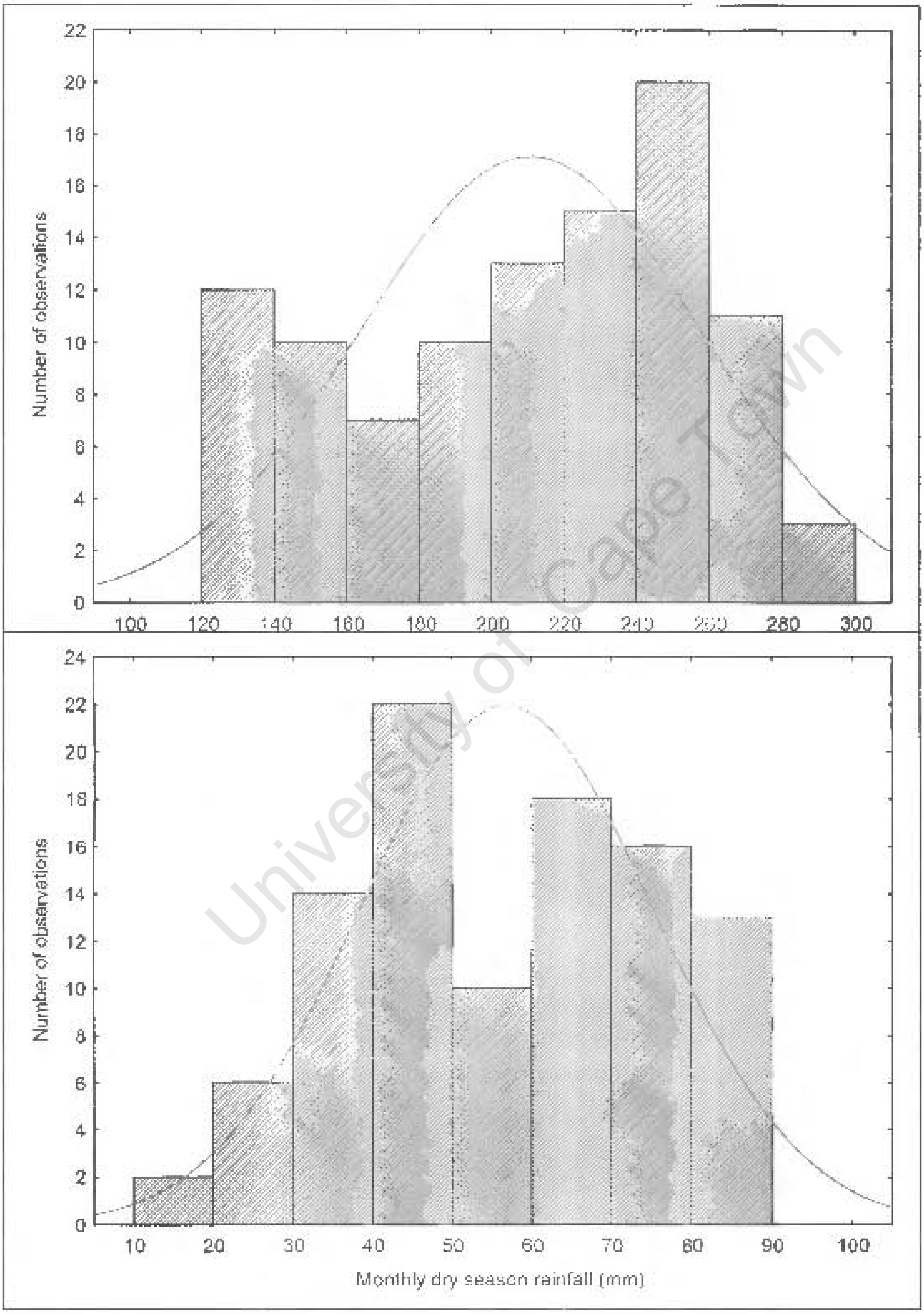
(Kamweneshe 1996, Howard and Aspinwall 1984), and the Okavango Delta in Botswana (Allsopp and Perlstein 1998, P. Hancock, pers. comm.). There is also some evidence that the Delta supported more breeding pairs in the past. P. Dutton (pers. comm.) claims that Wattled Cranes were "common" across the Delta floodplain in the 1960s and early 1970s Chapter 1). In 2000 and 2001, eight pairs of Wattled Cranes, three with chicks, were seen on the Savana River coastal floodplain, approximately 300 km south of the Delta. Several flocks of mixed non-breeding adult birds and juveniles have also been seen here. Local inhabitants note that Wattled Cranes have only recently begun breeding in the Savana floodplain and were previously observed only in flocks during the dry season (Florenço Kembo; pers. comm.), suggesting that some breeding birds that have abandoned territories on the Zambezi floodplain have moved into this region.

Beilfuss (2002) demonstrated that there is sufficient water available in Cahora Bassa Dam to generate a variety of flood pulses during the normal flood season from January to March. There is growing political and stakeholder support for flood releases (Beilfuss 1997, Beilfuss and Davies 1999), due largely to the potential economic benefits of prescribed flood releases for subsistence farmers and fishers in the lower Zambezi (Chilundo *et al* in press), the coastal prawn industry (Hoguane 1997), and ecotourism and safari hunting operations (P. da Silva pers. comm.). A process is now underway to apply the DRIFT (Downstream Response to Instream Flow Transformations) methodology to the lower Zambezi River and Delta (R. Beilfuss pers. comm.). Thus, there may be good prospects for improving the hydrological management of the Zambezi Delta in the future. Wattled Cranes may serve as a useful indicator species for assessing the value of flood releases for biodiversity conservation and management in the Delta given that their breeding responses are triggered on an annual basis by variations in water availability.

Summary

Given their specialized habitat and food requirements, it could have been predicted that profound changes to the Zambezi Delta's hydrological regime and herbivore megafauna would have had a severe impact on the region's Wattled Crane population. Upstream impoundments have, either directly or indirectly, resulted in floodplain aridification, a reduction in herbivory and an increase in fire frequency and extent. Qualitatively, it appears that this prediction is true for those cranes inhabiting areas of the Delta dependent on overtopping of the Zambezi River and its tributaries to inundate the floodplain. However, farther to the west, the floodplain below the Cheringoma escarpment has been largely unaffected by upstream impoundment of the Zambezi River – although cranes in this area have probably been impacted (to an unquantified degree) by fires. Nonetheless, based on present performance, this remaining population is healthy and acts as a source (albeit small) of export of adult cranes to other Southern African wetlands. Models predict that this population will continue to be self-sufficient even if the few remaining patches of suitable habitat under the influence of the Zambezi River are lost. This could change in future if plans to afforest parts of the Cheringoma floodplain catchment, or use the wetland for rice cultivation, go ahead. Should the performance of the Cheringoma cranes be compromised, or adult mortality rate increase, the population is predicted to enter negative growth.

Appendix (4) I. Randomly generated rainfall frequencies used in simulation models (with normal distributions superimposed).



Appendix (4) II. Equations used in model.

Equation 1; Figure 4.1 (used for Cheringoma sector):

$Y = 17.18.10^{-5}X^2 + 36.62X + 0.13$

Equation 2; Figure 4.2 (used for Zambezi Sector):

$Y = -17.62X + 1.12$

Equation 3; Figure 4.3 (used for Cheringoma sector):

$Y = 64.60.10^{-3}X^2 - 2.26X + 200.57$

Equation 4; Figure 4.4 (used for Zambezi Sector):

$Y = 0.12X - 26.75$

Summary and recommendations

Human activities ranging from dyke building to dam construction have dramatically reduced the volume, and changed the seasonality, of water flow in the lower Zambezi River. As a result, patterns of inundation of the adjacent floodplain have also changed, with extensive flooding occurring only in years of exceptionally high rainfall. Aridification of the floodplain and, the associated falling water table has led to changes in vegetation, with palm and acacia savanna encroaching into areas previously dominated by wetland plant communities and a reduction in the extent of floodplain grassland and papyrus communities.

The drying out of the floodplain has increased its accessibility to people and human pressures on the area have increased. Key consequences of this have been a) intensive poaching that has reduced the biomass of large grazers in the Delta by approximately 90% in the past 30 years, and b) an increasing extent and frequency of fires, most of which are started to improve access for fishers and hunters.

The loss of wetlands within the Zambezi Delta is highly likely to have affected populations of several wetland-dependent bird species, including the globally threatened Wattled Crane. Wattled Cranes, endemic to sub-Saharan Africa, are decreasing in numbers and are dependent on wetlands throughout the year. Not only are Wattled Cranes dependent on wetlands in the broad sense, but they also rely on a limited range of food types within these wetlands. In the case of the Marromeu cranes, the key food is tubers of the sedge *Eleocharis*. *Eleocharis* produces tubers in response to water stress caused by seasonal wetting and drying of the floodplain: tubers act both as water storage and reproductive organs. In the presence of prolonged drought or continuous inundation, *Eleocharis* does not produce tubers. Under natural flooding regimes, the spatial pattern of tuber production (and tuber density) changes over the seasons in response to wetting and drying cycles.

Currently, there are approximately 900 km^2 of *Eleocharis* beds on the Delta. Some 250 km^2 of *Eleocharis* in the eastern Delta fall under the direct influence of the Zambezi River: except for a few isolated pockets, these *Eleocharis* beds are ignored by the cranes, strongly suggesting that the changed hydrological regime has resulted in their failing to produce tubers. It can thus be reasonably concluded that the carrying capacity of the eastern Delta has been reduced as a result of changes to the hydrology (and that some displaced birds have moved to the Savana River floodplain). Farther west, below the Cheringoma Plateau, is an area of 650 km^2 of *Eleocharis* that forms the core of the Wattled Cranes' range within the Delta. These *Eleocharis* beds occur on the floodplains of channels, themselves connected to rivers flowing off the escarpment. These rivers are unregulated, resulting in a natural flooding and drying regime and hence tuber production by *Eleocharis*.

Within the Cheringoma site, crane numbers increase during the wet season prior to the onset of breeding. Territories are established at this time and eggs are laid after the peak of the floods. The number of pairs attempting to breed is positively correlated with wet season rainfall. In all years, some breeding attempts are abandoned early in the season (most being abandoned in dry years), with failed breeders either joining the "floater" population or moving away from the Delta (to destinations unknown). Breeding success, measured as chicks per pair, is highest in dry years. This suggests that a core area of optimal habitat exists and, in wet years, that some pairs occupy inundated territories that prove to be poor foraging areas when floods recede or where other sources of elevated mortality of eggs and young are operating.

Although the flooding regime of the Cheringoma site is fairly natural, reduction in grazer biomass has resulted in increased above-ground plant biomass. In other southern African wetlands, Wattled Cranes exist in close association with large herbivores, whose grazing increases accessibility of tubers to the cranes. In the Zambezi Delta, the cropping role of herbivores has been replaced by fire. Fire shortens the vegetation, improving foraging conditions for the cranes, but carries a major cost. Historically, by the time that natural fires started in the Delta, young cranes had fledged and could escape the fires. Today, fires occur over a longer period of the year and, although not proven, it seems highly likely that many small chicks perish in early dry season fires.

Simple simulation modelling suggests that, under present conditions, the Delta's Wattled Crane population is self-sustaining and may even export birds to other wetlands. Should the portion of the population under Zambezi River influence be lost, the Cheringoma population would continue to be self-sustaining, although exports to other sites would be small and irregular. However, the same models also suggest that should the mortality rate of adult cranes increase to equal that experienced by South African birds, the population would be destabilised and enter negative growth.

Although there are no existing plans to impound rivers flowing off the Cheringoma escarpment, proposals do exist for both rice cultivation in the wetlands and for partial afforestation of the catchments with eucalypts. The former would reduce the area of *Eleocharis* beds and hence the area's carrying capacity for cranes. Exotic plants increase transpiration and intercept rainfall. This leads to a decrease in of local runoff (van Wilgen *et al* 1996). A single Eucalyptus in average, use 46 litres of water annually. Even if planted at the minimum density of 316 trees/ha (Dye *et al* 1997), a 10 000 hectare plantation would result in 145 360 m³ of water being lost per year. This volume of water loss would almost certainly negatively affect the pristine portion of Wattled Crane habitat on the Cheringoma floodplain. Mondi Company was proposing to plant 60 000 – 70 000 ha (P. Dutton, pers.comm.).

More dams are planed for the Zambezi River downstream (Li-EDF-KP Joint Venture Consultants 1999). The proposed Mepanda-Uncua Dam would result in significant loss of water through evaporation from the reservoir. This dam would also impound the remaining sediments coming from Luia River. Therefore, more negatives impact on Delta, specially the areas influenced by the Zambezi, can be expected.

At present, the only area of the Zambezi Delta in which abundant, flood-dependent bird and animal life persists is the area below the Cheringoma escarpment. Should the hydrology of this region change, the effect on the Delta as a regional reservoir of biodiversity would be catastrophic. Apart from continued protection of the Cheringoma catchments, the only insurance against such a catastrophe lies in restoration, or at least partial restoration, of those areas of the Delta under the direct influence of the Zambezi and its tributaries. Recent studies have shown that Cahora Bassa Dam contains enough water both to satisfy hydro-electric requirements and to permit an annual, medium-sized flood release (Beilfuss 2002).

Many of the Delta's human inhabitants (e.g. fishers) are dependent or partially dependent on wetland resources. Much of the region's biodiversity is entirely dependent on these resources. Consequently, such releases should be considered a priority before the effects of aridification and associated landscape change become irreversible.

The way forward

The costs of annual monitoring of crane (and other wildlife) numbers and performance in the Zambezi Delta are high. Indeed, these costs influenced the way in which the later surveys of this study were conducted. Given that the area below the Cheringoma escarpment has now been identified as the key biodiversity hotspot for wetland-dependent wildlife, efforts should be concentrated here, especially should rice or eucalyptus planting take place. In terms of the Wattled Cranes, the most valuable data would be obtained from aerial surveys in November, when breeding population size and success (rather than breeding effort) can be determined.

Monitoring the landscape-level changes of the eastern Delta might best be achieved using satellite imagery: unless patterns of water management change, this area's continued degradation is inevitable. However, should an agreement be reached whereby annual releases from Cahora Bassa are approved, aerial monitoring of the effects of such management would become a priority.

On a none positive note, the Zambezi Delta provides an opportunity for scientists, dam managers and all stakeholders to co-operate in optimizing multiple use of Cahora-Bassa Dam. Besides the hydropower production, Cahora Bassa can offer increased benefits to local communities (e.g. Gammelsrod 1996, Hoguane 1997, Beilfuss *et al* 2002) as well as the environment without reducing its power output (e.g. Beifuss and Davies 1999, Beilfuss *in press*). Cahora Bassa Dam was constructed as part of a multpurpose river basin development scheme, but has never been managed as such. The improved management of the Zambezi waters to benefit a wider array of stakeholders would unquestionably result in important economic gains for the regional and national economy (e.g. Gammelsrod 1996, Hoguane 1997, Beifuss 1999 and Beilfuss *et al* 2002). Prescribed flooding in the lower Zambezi system is a fundamental component of any program that aims to alleviate poverty and preserve biodiversity in the Zambezi Delta.

To date, Mozambique is not a signatory to the Ramsar Convention. Thus, although the Zambezi Delta unquestionably satisfies many of the biological criteria for registration as a "Wetland of International Importance" under the Convention, it cannot be registered as such. Mozambique's recognition of the Ramsar Convention should also be considered as a priority.

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This thesis is part of a comprehensive program for the integrated development and ecological restoration of the lower Zambezi basin. The overall program, an interdisciplinary collaboration among Mozambican, South African, and North American researchers and decision-makers, aims to conduct fundamental hydrological, socio-economic, and ecological research to test whether artificial flood releases are an effective tool to restore and enhance key ecological processes and local production systems in the lower Zambezi system. The program also aims to assess the financial feasibility of improved water management and to provide specific policy recommendations for the sustainable and equitable management of Zambezi waters in the future. The International Crane Foundation initiated the program in 1995.

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