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Richard Beilfuss
International Crane Foundation

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Distribution, structure and simulation modelling of the Wattled Crane population in the Marromeu Complex of the Zambezi Delta, Mozambique

Carlos M Bento[1], Richard D Beilfuss[2]* and Phillip AR Hockey[3]
[1] *Museu de História Natural, Eduardo Mondlane University, Praça Travessia do Zambeze, 104, Maputo, Mozambique*
[2] *International Crane Foundation, E11376 Shady Lane Road, Baraboo, Wisconsin 53913-0447, USA*
[3] *Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa*
* *Corresponding author, e-mail: rich@carrfoundation.org*

The status of the Vulnerable Wattled Crane (*Grus carunculatus*) in Mozambique is poorly known, but historical accounts indicate that the species was previously more abundant and widespread than today. Annual surveys during 1995–2002 suggest a core population of about 120 breeding pairs remains in the Zambezi Delta region. Wattled Cranes in the delta are exclusively associated with sedges of the genus *Eleocharis*, the tubers of which provide the adult cranes' main food supply. The main *Eleocharis* areas in the delta, and those supporting the highest density of Wattled Cranes, occur below the adjacent Cheringoma escarpment, where unregulated streams flow onto the floodplain. These wetlands experience some seasonal inundation in all years — conditions essential for the production of underground tubers — and high soil penetrability to enable the cranes to extract tubers. *Eleocharis* tuber production and soil penetrability is extremely low in the remaining vast areas of the delta that no longer receive regular annual flooding due to regulation of the Zambezi River. Significant differences in crane density between the *Eleocharis* beds of the Cheringoma and Zambezi floodplains suggest that the carrying capacity of the delta for cranes has been reduced. Simulation modelling 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. Restoration of the hydrological conditions in the delta may have global implications for the species, however. In 1990, an estimated 2 570 Wattled Cranes (more than 30% of the global population) were observed in the delta. This was likely an occasional flock from elsewhere in southern Africa, as prolonged regional drought resulted in failed floods, low tuber productivity and relatively impermeable soils in the region.

Introduction

The Wattled Crane (*Grus carunculatus*) is a globally Vulnerable resident of sub-Saharan Africa (BirdLife International 2000). Wattled Cranes are the most wetland-dependent of Africa's cranes (Meine and Archibald 1996). Three populations are recognised. The core population occurs in southern Central Africa on the primary floodplains and *dambos* of the upper Congo, Zambezi and Okavango River basins. More isolated populations occur in Ethiopia and South Africa, with the Ethiopian population likely to be a distinct subspecies (Jones 2003).

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 (West 1977). In central Mozambique, the species was considered 'common' in the Zambezi Delta in the 1970s (P Dutton *in litt*. to RDB) and more than 2 500 birds were reported in 1990 (Goodman 1992).

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 and low reproductive output) and specialised habitat requirements (Johnsgard 1983). When hydrological conditions are not satisfactory at a particular location due to drought, flooding or inappropriate water management, most Wattled Cranes fail to initiate nesting (Douthwaite 1974, Konrad 1981). The availability of the Wattled Crane's main food source, underground tubers of spike rushes (*Eleocharis* spp.), water lilies (*Nymphaea* spp.) and various sedge species (especially *Cyperus* spp.), is also negatively affected by any reduction in the regular annual cycle of flooding and drying (Beilfuss 2000).

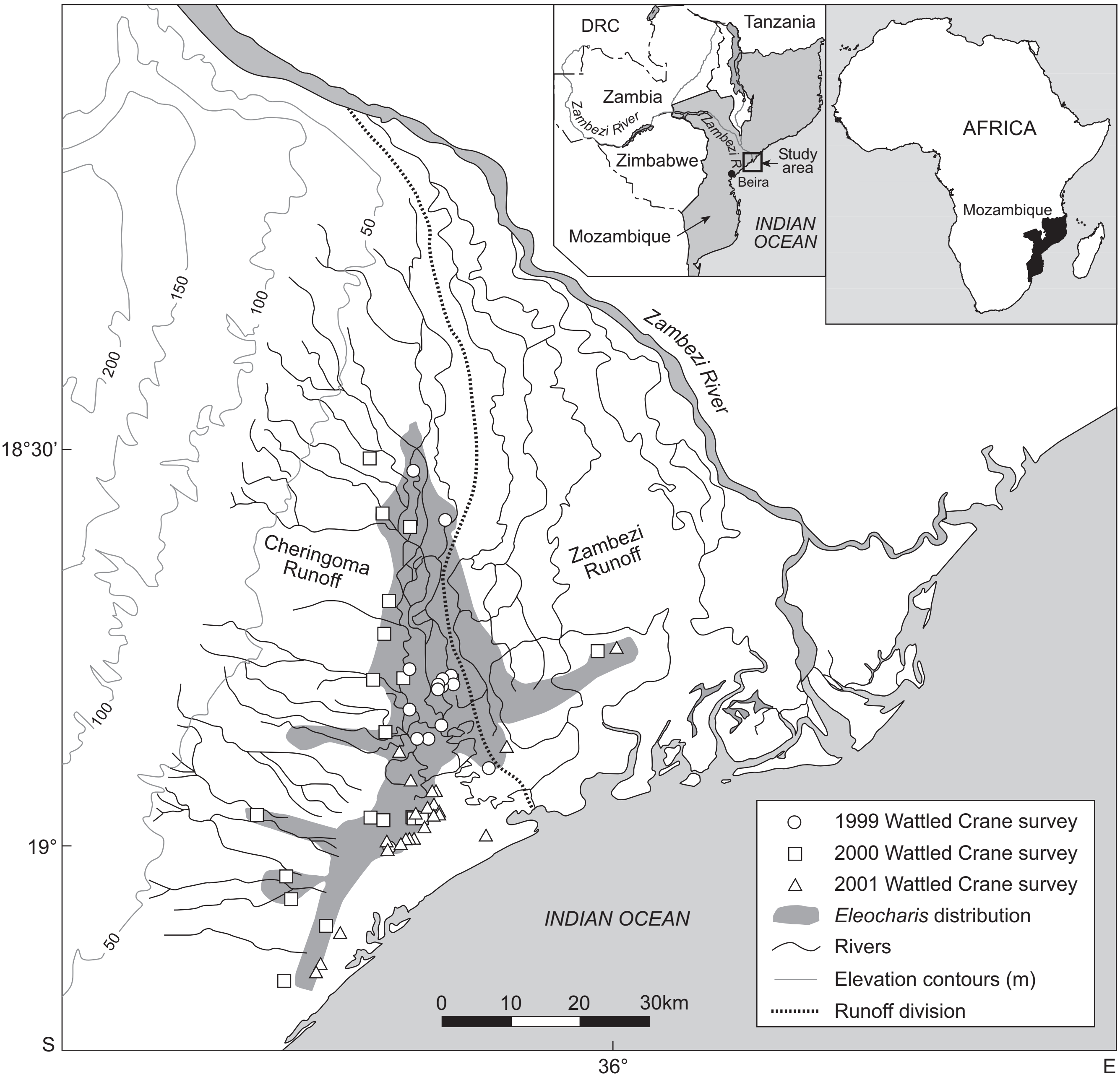
This paper describes the population status and distribution of Wattled Cranes in the Marromeu Complex, with emphasis on the impacts of hydrological and ecological changes on the breeding and feeding ecology of the birds. We hypothesise that Wattled Crane breeding success is low in the Marromeu Complex compared to other less disturbed wetlands in southern Africa based on changes in hydrological conditions (and associated changes in patterns of fire and grazing). We also hypothesise 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. Thirdly, we hypothesise 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.

Methods

Study area

The Zambezi Delta is located on the Indian Ocean coast in central Mozambique (18°00'–19°00'S, 35°00'–36°05'E). It lies at the downstream terminus of the Zambezi River, with a catchment area of 1 390 000km² extending over portions of eight different countries.

The study site includes the south-bank floodplains of the Zambezi Delta and the adjacent Cheringoma escarpment, in an area known as the Marromeu Complex (Figure 1). The 14 000km² Marromeu Complex was designated recently as a 'Wetland of International Importance' under the Ramsar Convention (Beilfuss and Bento 2003). The complex comprises the protected Marromeu Buffalo Reserve (*Reserva especial de Marromeu*), the four surrounding hunting concessions (*Coutadas* 10, 11, 12 and 14), and coastal dunes and mangroves. The delta is extremely flat and poorly drained, with widespread areas underlain by hydromorphic vertisols and gleys that support



Elevation data derived from 3 Arc Second SRTM data; United States Geological Services 2002
Reprocessed by the International Crane Foundation 2004

Figure 1: Overall Wattled Crane distribution from 1999–2001 and extent of *Eleocharis* on the Cheringoma escarpment and Zambezi Delta floodplain of the Marromeu Complex

a variety of wetland plant communities, including palm savanna, flooded grassland, papyrus swamp and reed swamp (Beilfuss *et al.* 2000, Beilfuss 2001). At the western margin of the delta plain, the Cheringoma escarpment rises gradually to a crest of 394m asl, where it forms the eastern side of the Rift Valley. The escarpment is overlain by Quaternary sands and supports a mosaic of dry forest with shallow wetland pans and miombo woodland with wetland slacks (Tinley 1977). The total catchment area of the Cheringoma escarpment draining to the Marromeu Complex is approximately 8 300km^2 (Beilfuss 2001).

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. The main rainy season usually occurs over a 4–6 month period between October and April, and is characterised by brief periods of thunderstorms followed by periods of drier weather. Mean annual rainfall ranges from 1 000mm at the apex of the delta to more than 1 400mm along the coast, and there is considerable inter-annual variation (Beilfuss 2001).

Surveys

Six aerial surveys were conducted over the Marromeu Complex between 1995 and 2001, targeting either the end of the wet season or the latter part of the dry season (Beilfuss and Allan 1996, Beilfuss and Bento 1998, Bento 2002). All surveys were conducted in a Cessna 210 aircraft, flown 90m above ground level at an average speed of 100 knots (177km h^{-1}), with two observers located on each side of the plane. Transect lines were orientated approximately parallel to the coast and spaced 4km apart with a 1km observation distance on each side of the plane, providing 50% coverage of the complex. All Wattled Crane observations were recorded either as singletons, pairs, family groups or flocks. Wattled Crane locations were marked using an in-cockpit GPS. For each Wattled Crane location we described the vegetation community type, dominant plant species, and presence or absence of *Eleocharis* species.

Two ground surveys were undertaken to observe Wattled Crane feeding activity in 1999 and 2000. Surveys were conducted 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 accessible during the early to late dry season, using an amphibious vehicle. Food plants were collected, labeled and pressed for identification at Eduardo Mondlane University in Maputo. Detailed studies of Wattled Crane feeding activity and productivity of *Eleocharis* tubers in relation to flooding duration, water depth and soil penetrability are described elsewhere (Bento 2002).

Population modelling

Wattled Crane population models were constructed using Stella Research Software 5.1.1 (HPS 1996). A simple simulation model was developed for the entire Marromeu Complex using average relationships between rainfall, breeding numbers and productivity (number of chicks observed per breeding pair). In a second set of simulations, the Cheringoma escarpment and delta floodplains were modelled separately, driven by site-specific regressions of population parameters on rainfall. This enabled more detailed comparison of the contribution made by each sector to the total population. Flow diagrams summarising the models' structures are provided in Bento (2002).

The model was initiated with a stock of 240 breeders, based on 120 pairs observed on territories during the wet season, 11 one-year-old chicks and 15 floaters (non-breeding birds). Mature birds were defined as being more than five years old. 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 Crane adults or chicks in the Marromeu Complex. 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 conservatively assumed to be 3%. Mortality rate for first-year birds was assumed to be 9%, decreasing by 1% annually. Mortality rate in the sixth year is thus 4% (Bento 2002). This value of 4% was also applied to members of the floater population more than five 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 month^{-1}, 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. All models generated two key outputs on an annual basis: size of the breeding population, and size of the floater population.

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 the 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

Wattled Crane distribution and density

The combined results of all six surveys conducted between 1995–2001 provide an overview of Wattled Crane distribution in the Zambezi Delta. The occurrence of cranes is restricted to seasonal floodplain grassland where there are patches of *Eleocharis* (*E. acutangula* and/or *E. dulcis*) (Figure 1). The total area of *Eleocharis* within the Delta is approximately 900km². The beds located below the Cheringoma Plateau account for 650km² (72% of the total area). Further east, in the area influenced by the Zambezi River, there are 250km² of *Eleocharis* (28% of the total), mostly near the coast. In the area influenced by the

Cheringoma rivers, Wattled Crane densities were 0.12, 0.15 and 0.31 birds 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 birds km^{-2} in 1999 (Table 1). Very few Wattled Cranes were observed in areas of the Marromeu Complex lacking *Eleocharis* species.

A comparison of the 1999, 2000 and 2001 aerial surveys shows that, although in all surveys Wattled Cranes were confined to the base of the Cheringoma escarpment 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. 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*. 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. In 2001, crane distribution across the Cheringoma *Eleocharis* beds changed again, with the birds being concentrated in the south and closer to the sea.

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*. Large foraging flocks of non-breeding Wattled Cranes also occur on *Eleocharis* beds at the end of the dry season and early wet season.

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). No birds were seen in the wet season of 2001, when water levels were exceptionally high. End of 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 (Table 3). 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.

There was a slight increase in the total number of cranes estimated to be in the Marromeu Complex between 1995 and 1997 (Table 3). However, this difference was due mostly to an increase in the number of flocking birds. Given the errors associated with estimating numbers in non-breeder flocks that may range over vast areas, the difference — an increase of 9.9% — is probably insignificant.

Table 1: Estimated numbers and density (birds km^{-2}) of Wattled Cranes, including chicks, associated with sedges of the genus *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 km^{-2}	0.12	0.02
2000 Birds	97 (97%)	3 (3%)
Density km^{-2}	0.15	0.01
2001 Birds	203 (94%)	14 (6%)
Density km^{-2}	0.31	0.06

Table 2: Summary of the counts of Wattled Cranes during three aerial surveys as well as the estimated number of pairs in the late wet season

	March 1995	May 1997	April 2001
Aerial coverage (%)	50	50	50
Pairs on territories	58	60	0
Chicks	0	0	0
Number of unpaired individuals (individuals in flocks)	40	59	0
Estimated number of pairs	116	120	0
Minimum total population	272	299	0

Although the number of pairs attempting to breed increased with increasing mean monthly wet-season rainfall between 1999 and 2001, even in 2001 following massive flooding in the Delta only 68% of the estimated pool of 120 pairs (based on surveys from 1995–1997) attempted to breed. The increase from 12 to 21 observed 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^{-1}; 1999) occurred in the year of lowest rainfall when fewest birds were breeding. In the higher rainfall years of 2000 and 2001, breeding success ranged from 0.24–0.27 chicks pair^{-1}, averaging only 61% of the breeding success in 1999 (Table 3).

Simulation modelling

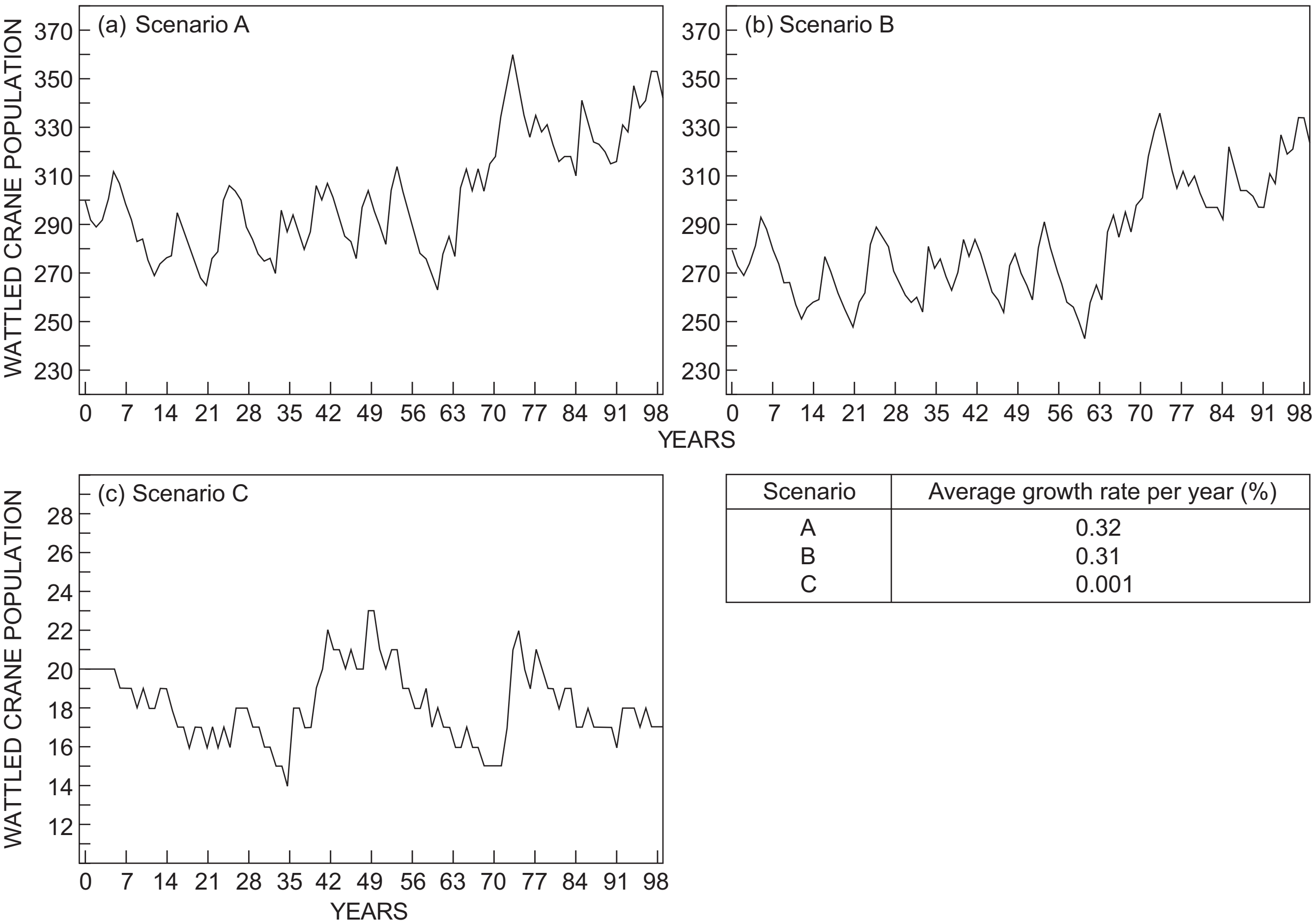
The first scenario (A, current baseline conditions) predicts an average population growth rate of 0.32% per year (Figure 2a). Should the Zambezi floodplain population be lost (scenario B), the Wattled Crane population is still self-sustaining with slightly lower growth rate of 0.31% per year (Figure 2b). Although the Delta's population growth rates under scenarios A and B differ slightly, the average number of chicks produced annually differs significantly ($t = 4.64$; $p < 0.05$; $n = 101$). If there is no contribution from pairs breeding on the Cheringoma floodplain, the population is self-sustaining (growth rate of 0.001% per year), but with very small numbers it is potentially at risk from stochastic events (Figure 2c).

The modelled population of breeding adults fluctuates annually, with new breeders recruiting from the floater population during high-rainfall years and the reverse

Table 3: Wattled Crane population size in the late dry season (November) of 1999–2001, together with estimates of their productivity and measures of rainfall

	1999	2000	2001
Coverage (%)	50	60	50
Observed pairs	12	25	41
Estimated numbers of pairs	24	42	82
Estimated numbers in non-breeding flocks	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)



Scenario	Average growth rate per year (%)
A	0.32
B	0.31
C	0.001

Figure 2: Wattled Crane population trends including breeding adults, floaters and juveniles/immatures less than six 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)

occurring during years of low rainfall. If the *status quo* persists, or if only Cheringoma birds are present, the number of non-breeding adults always exceeds the number of breeders at the end of the dry season. If the Zambezi population alone remained, there would be many years in which no birds bred. Similarly, loss of this population would have a very small effect on total chick production in the Delta. Because the Cheringoma and Zambezi populations respond

Table 4: Population responses of the 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	–

differently to dry-season rainfall, numbers of chicks produced annually by the two populations are not closely synchronised.

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).

Both sectors respond positively to wet season rainfall in terms of the number of pairs attempting to breed and total chick production in the population. On the Cheringoma, productivity per breeding pair is highest in wetter years, but on the Zambezi, it is maximal in dry years.

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. A similar dependence on carbohydrate-rich *Eleocharis* tubers has been observed for Brolga (*Grus rubicundus)* and Eastern Sarus Cranes (*Grus antigone sharpii)* (Lavery and Blackman 1969, Meine and Archibald 1996) as well as Magpie Geese (*Anseranas semipalmata)* (Frith and Davies 1961). In the Delta region, the main *Eleocharis* areas and those supporting the highest density of Wattled Cranes lie 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 that are the means by which *Eleocharis* survives the dry season (Li *et al.* 2000). 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. 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.

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 (Bento 2002). 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 such as 2001, the floodplain margins are used more extensively, presumably because core areas are too deeply inundated. In wet years, the timing of breeding is more staggered (and the breeding season spread over a longer period of time) than in dry years. Pairs that occupy floodplain-edge territories first rear their chicks earlier than pairs using the core of the floodplain; the latter pairs can only take occupancy after flood levels have receded.

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 (Tables 2 and 3). As early in the breeding season as May–June, many pairs abandon their breeding attempts and join flocks of other failed or non-failed breeders. Many of these birds, in turn, move south along the coast to other seasonally flooded areas and a few may attempt to breed in these secondary habitats. That only a portion of the population should breed in any one year is not unusual for the species. On the Kafue Flats, Zambia, in 'normal' flood years about 40% of the population attempts breeding; in very dry years, this may decrease to as little as 3% (Douthwaite 1974). In Botswana, only 16%, 6%, and 10% of the population bred in 2001, 2002, and 2003, respectively (Motsumi *et al.* 2003).

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. This implies that 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. Alternatively, 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 (Table 3), the second explanation is the most parsimonious. Whilst rainfall strongly influences the numbers of pairs attempting to breed at Cheringoma, it has little or no influence on the numbers attempting to breed on the Zambezi (Table 3). 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, these beds may not persist for long.

Based on relatively few aerial surveys it is difficult to assess the existence or otherwise of population trends, especially given that non-breeders can wander considerable distances. In the late wet season of 1995 and 1997, the minimum population (excluding chicks) was 270–300 birds (Table 2). Numbers undoubtedly fall during the dry season because of seasonal emigration in response to falling water levels (Table 3). 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 3). 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 below). 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 (Tiffen and Mulele 1994) that affected most of the key breeding sites for Wattled Cranes. The humid delta was relatively less affected than inland areas. In the late dry season of 1990, 2 570 Wattled Cranes were counted in the Delta, many 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 3). 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. Of those pairs that did remain to breed between 1999 and 2001, productivity ranged from 0.24 (2000) to 0.42 (1999) fledglings per breeding pair per year. Breeding population size and total chick production was positively linked to rainfall. Highest breeding success per pair 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. Firstly, 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. Secondly, nests and chicks are more accessible to predators in wet years; intuitively, the opposite would be predicted, as is the case with African Jacanas (*Actophilornis africana*) (Tarboton 2001). Thirdly, increased primary production during the wet years increases the fuel load and thus the extent and intensity of fires. In the third case, 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 (Beilfuss and Davies 1999), even following good rains the floodplain surface dries out much faster than it would have done in the past. Preimpoundment, the floodplain was inundated for nine months of the year (Beilfuss 2001) 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 and is worthy of a separate investigation.

Changes in the abundance of large herbivores also affects Wattled Crane distribution and productivity. Grazers such as lechwe species, zebras and buffalo 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, Bangweulu Swamp and Luiwa Plain, Wattled Cranes and grazers occur in close association (e.g. Konrad 1981). On the Zambezi Delta, the numbers of grazers have been reduced dramatically since the late 1960s, mostly because of illegal hunting (Anderson *et al*. 1990). In 1968 the combined numbers of buffalo, waterbuck, zebra, hippo and elephant were about 61 100 (Tinley 1969), but aerial surveys conducted in the late 1990s estimated the herbivore population at less than 8 500 (Dutton 2002). 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 to cranes, 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 than birds on the Zambezi (Kamweneshe and Beilfuss 2002; Motsumi *et al.* 2005).

Simulation modelling 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 individuals per year (Figure 2a). 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 a growth rate of 0.31 birds per year and is predicted to recover from the loss of Zambezi birds (Figure 2b). However, under this scenario, the Delta's productivity is slightly lower.

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 2b). Although scenario C models predict the Zambezi population to be stable, its very low numbers (Figure 2c) would make this population vulnerable to catastrophic events.

Although the Delta's Wattled Cranes are currently self-sustaining, our 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. Furthermore, 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 2001). Meine and Archibald (1996) note that small crane populations are particularly vulnerable to natural disasters. The population of Whooping Cranes in Louisiana (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 at 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). The mortality rate in South Africa is almost certainly higher than in the Delta, because the Delta has relatively few power lines (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.

Conservation implications

The global population of Wattled Cranes is decreasing (Beilfuss *et al*. 2007) 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 2 500 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. 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 (Kamweneshe and Beilfuss 2002) and Bangweulu Swamps in Zambia (Kamweneshe *et al.* 2003), and the Okavango Delta in Botswana (Motsumi *et al.* 2005). 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. In 2001, eight pairs of Wattled Cranes, three with chicks, were seen on the Savana River coastal floodplain approximately 300km 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 (2001) 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 1999, 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.* 2002), the coastal prawn industry (Gammelsrod 1996), and ecotourism and safari hunting operations (Anderson *et al*. 1990). A process is now underway to assess the environmental flow requirements of the lower Zambezi River and Delta. 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.

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