Chapter 5: The influence of elephants on *Faidherbia albida* trees in the northern Namib Desert: a reappraisal.

Abstract: Elephants (Loxodonta africana) are well known for the tremendous effect they can exert on their habitat. The Namibian media expressed concern in the early 1980's regarding the influence of desert-dwelling elephants on vegetation within the lower Hoanib River in the northern Namib Desert. A subsequent survey reported no detrimental effects, although my observations in 1994 suggested significant tree damage had occurred since. I resurveyed the area in 1995 to quantify the changes that had occurred in the past 12 years, and considered several hypotheses to explain them. I found that a significant change had occurred in the size structure of the Faidherbia albida forest. Of the 638 trees I examined within the lower Hoanib River, 196 (30 %) were dead and exhibited evidence suggesting they had been killed by elephants. Of the 196 dead trees, 142 (73 %) were <20 cm in diameter. As a result of this selective feeding and associated lack of recruitment, the current size distribution of trees is strongly skewed towards older trees, likely to be more susceptible to die-off should environmental conditions change significantly. The cause of this change in foraging is unclear. Elephant density has not increased nor has their been any significant hydroclimatic variation since the early 1980's. Subtle shifts in resource use patterns, possibly triggered by prior human-associated disturbance (primarily poaching), may be responsible for the observed decline in tree survival and recruitment. In combination with proposed hydrologic alterations of the Hoanib River associated with agricultural developments, this skewed age structure could result in a massive die-off of Faidherbia trees along the lower river.

Key words: ephemeral rivers, disturbance, age structure, compression hypothesis, riparian vegetation, floods, Africa

Introduction

The African elephant, *Loxodonta africana* Blumenbach, has long been recognized as a major force affecting vegetation communities throughout its range (Laws 1970). In particular, when combined with human-induced shifts in population density and available foraging area, such effects can be severe and result in the decimation of affected vegetation (Anderson and Walker 1974, Barnes 1983a & b). Because of their comparatively low productivity, dryland vegetation communities may be particularly susceptible to damage by foraging elephants, although there are many conflicting views (see Behnke et al. 1993 for a recent review). Thus, the desert-dwelling elephants of the northern Namib Desert, the only remaining desert elephant population in the world, presumably have great potential to degrade their habitat.

The Namib elephants, particularly those in the most arid regions, subsist in a series of ephemeral river courses and associated floodplains that provide food and water resources within an otherwise hostile landscape (Viljoen 1989a, Viljoen 1989b). In the early 1980's, concern was expressed by the Namibian media regarding the potential effect of the elephants on the riparian vegetation within these rivers, particularly the large Faidherbia albida (Del.) A. Chev. trees that grow in and along the channel of the Hoanib River in northwestern Namibia (Schoeman 1982). Faidherbia albida, formerly Acacia albida Del., is a large tree, reaching a height of over 15 m and a diameter in excess of 2 m within the Hoanib River. These stately trees produce large amounts of fruits, and a single tree can produce more than 200 kg of the dry indehiscent pods in a single year (Jacobson Ch. 2, CTFT 1989). Aside from their aesthetic appeal, the trees have great ecological importance as a source of forage, providing pods, foliage, and bark for the region's elephants. Despite the concern that the desert-dwelling elephants may have been having an adverse effect on the trees, a study completed in 1983 concluded that there was no evidence of such an effect (Viljoen and Bothma 1990a). Although trees were occasionally ring-barked, having the bark removed from the entire circumference of their trunks, the frequency was estimated to be less than the recruitment rate and not significant to the long-term viability of the population.

I first visited the river in 1994, and my observations made me question whether this conclusion was still valid. Although Viljoen and Bothma (1990a) reported no negative effect on the river's vegetation other than the occasional debarking of Faidherbia trees, I observed evidence that elephants were actively breaking down Faidherbia trees up to ~40 cm in diameter. I thus initiated a study to reexamine the influence of elephants upon the recruitment and size structure of Faidherbia albida trees within the lower Hoanib River. My objectives were to resurvey the reach of the river surveyed by Viljoen and Bothma (1990a), quantifying the changes in stand structure occurring in the past 12 years; to examine several hypothesis to explain the observed differences, with particular attention to the influence of poaching on the spatial patterns of foraging; and to discuss the findings

with respect to current land use patterns in the region and the conservation of the elephants and their habitat.

Methods

Study Area

The Hoanib River drains a catchment of ~17,000 km² in northwestern Namibia, flowing a distance of ~300 km from its headwaters near the Etosha National Park, westward to the Atlantic Ocean. *Faidherbia albida* trees occur most of the river's length, but reach their greatest size and abundance within the lower 100 km of the river laying within the Namib Desert. The trees' survival depends upon the occasional floods that originate within the upper reaches of the catchment, bringing water and nutrient-rich sediments to the lower river (Jacobson, Ch. 1 & 4). While floods have flowed occurred in the lower Hoanib every year since record keeping began in 1977, their duration and magnitude are highly variable. Floods are an essential source of water, as the median annual rainfall along the lower river decreases from ~75 mm at Sesfontein, some 100 km inland, to <20 mm at the coast. Germination and recruitment of woody species, as well as annual grasses and forbs, is therefore almost entirely dependent upon floods.

The river traverses a mountainous landscape interspersed with large valleys and sandy or stony plains. A series of small tributaries enter the river along its lower 100 km, and although they contribute little to the annual runoff, they serve as important corridors for wildlife moving across the region's rugged landscape. This is particularly true for the mainstem of the Hoanib River, which is the region's principal east-west wildlife corridor. Approximately 20 km from the sea, the river's course is blocked by the coastal dunefield of the northern Namib Desert. Only in years of exceptional flooding does the river reach the sea, an event that has occurred only four times in the past 33 years (1963, 1982, 1984, and 1995). In most years floodwaters are impounded by the dunes and spread across a broad plain, commonly referred to as the 'Hoanib floodplain' (Viljoen 1989a). This terminal floodplain is an important resource for the region's wildlife during periods when floods have stimulated the growth of grasses and forbs and serves as a key wetseason resource patch for the region's elephants (Viljoen 1989a, Viljoen 1989b).

Viljoen (1989b) studied the seasonal distribution of elephants within the lower Hoanib River and noted distinct shifts corresponding to changes in food and water availability. In particular, the wet season core areas for two family groups centered on the lower Hoanib River floodplain, while their dry season core areas shifted to wetlands in the Hoarusib River, ~60 km to the north, and the Dubis wetland, ~65 km upstream in the Hoanib River. These wetlands occur where variations in bedrock geology result in groundwater discharge, producing isolated reaches of surface flow up to several hundred meters or more in length.

The Dubis wetland is an important focal point for elephants within the Hoanib River, providing a key dry-season water source. The concerns expressed over the potential effect of elephants upon the river's vegetation (Schoeman 1982) focused largely on the 65-km reach from the Dubis wetland downstream to the floodplain. The subsequent study by Viljoen and Bothma (1990a) examined the effect of elephants upon the *Faidherbia* trees within this reach.

Vegetation Surveys

Viljoen and Bothma (1990a) used several methods to examine the effect of elephants upon the vegetation within the lower Hoanib River, including an examination of multiple sets of aerial photos for changes in the number of large trees, measures of selected trees to assess age structure and mortality patterns, and transect surveys to assess the extent of bark removed. As the precise locations of Viljoen's surveys were unclear, I distributed my survey effort evenly over the 65-km reach between the Dubis wetland and the floodplain, which was divided into eight ~8-km sections. I initially planned a complete survey of the *Faidherbia* trees within the first kilometer of each section, but a preliminary survey revealed that the density of trees downstream of the wetland was less than 2 trees km⁻¹ for the first 12 km. Thus, I divided this 12 km reach into two 6-km sections, and conducted a complete survey of each section. The remaining 53 km was divided into six equal sections, and the first kilometer of each section was surveyed.

Within each survey section the total number of living and dead *Faidherbia* trees was counted. Dead trees included standing dead, as well as the stumps of broken-off trees. The stem diameter at ~1.5 m height was measured on both living and standing dead trees, and in cases where cespitose clumps occurred, the diameter of each stem was measured separately. For stumps, the diameter was also measured at 1.5 m, or at its highest point if less than 1.5 m tall. Standing dead trees were examined to determine if ring-barking was the probable cause of death. The percentage of bark removed relative to the tree's circumference was estimated for all live and dead standing trees. Trees exhibiting any debarking were also examined for signs of wood boring beetle infestations. All stumps were examined for the presence of root or stem sprouts. Finally, following the 1995 floods, sections were resurveyed to record the number and size of trees removed by the floods.

Results

The current size distribution of *Faidherbia* trees in the lower Hoanib River differs markedly from that observed in 1983 by Viljoen and Bothma (1990a) (χ^2 =145.3, p<<0.001, df=5) (Table 1). In particular, the number of 2-20-cm trees (0.2 %) measured in 1995 is more than two orders of magnitude below the 30.1 % reported from the 1983 survey. Of the 638 trees examined within the lower Hoanib River, 196 (30.7 %) were

dead and exhibited evidence suggesting they had been killed by elephants. In contrast, in 1983 a sample of 238 *Faidherbia* trees contained 14 (5.9 %) trees killed by elephants (Viljoen and Bothma 1990a). The average diameter of the dead trees in the 1995 survey was 21 cm (±12.5), ranging from 2-64 cm. The diameter of the 442 live trees averaged 78.4 cm (±33.1), ranging from 18-226 cm.

Viljoen and Bothma (1990a) reported that the size distribution of Faidherbia trees in 1983 conformed to a "reverse J-shaped curve ... indicative of a climax population," concluding that, "the Acacia albida population in the Hoanib River is a healthy climax and stable population." In contrast, the current distribution exhibits a pronounced absence of trees in the 2-20-cm size class and a decrease in the 20-40 cm class as well. Of the 638 trees measured, 196 (30.7 %) were dead, and 142 (72.5 %) of these were within the 2-20-cm size class. The percentage of dead trees within each reach ranged from 12.5 to 26.3 %, and the mean of the three reaches within 20 km of the Dubis wetland (20.8 %) did not differ from that of the lower three reaches (21.3 %), 28-44 km downstream .

The incidence of ring-barking was low; only 5 (0.9 %) Faidherbia trees from a sample of 535 mature trees were ring-barked, comparable with that recorded in 1983 (Viljoen and Bothma 1990a), when 5 of 213 (2.3 %) individuals had been killed through ring-barking. The five ring-barked trees in the 1995 survey averaged 46 cm (±4.6) in diameter, compared to an average of 20.7 cm (±12.1) for the 191 tree stumps. Viljoen and Bothma (1990a) reported that 31.6% (45 of 142) of a sample of mature Faidherbia trees had >20 % of their bark removed by elephants. In contrast, I observed that elephants had removed >20 % of the bark from 74 % (124 of 168) of mature trees. Although Viljoen and Bothma (1990a) reported that wood borers were absent from bark-damaged trees in the Hoanib River, they had colonized 4 of 168 (2.4 %) living trees at sites of bark damage.

Debarking stimulated a dramatic alteration of the vascular cambium in 33 % of a sample of 402 mature *Faidherbia* trees, resulting in the development of numerous deep convolutions, which ran parallel to the longitudinal axis of the trunk. These folds in the surface of the trunk appeared to offer some protection from ring-barking, as bark could only be removed from the outermost surface of the folds. The frequency of their occurrence decreased with distance from water. Within 12 km of the Dubis wetland, 76 % of the mature *Faidherbia* trees exhibited these convolutions, dropping to 9 % at a distance of 44 km. Viljoen and Bothma (1990a) did not report these features, which may be a recent development in response to the increased incidence of debarking.

I found no evidence that elephants were uprooting trees in the Hoanib River. Viljoen and Bothma (1990a) reported a similar absence, in contrast to reports from savanna habitats (Laws 1970). As suggested by Viljoen, the absence of uprooted trees, despite the heavy browsing pressure, may be a function of *Faidherbia albida's* strong tap root (CTFT 1989). The stability that this rooting structure confers may actually

contribute to stem breakage, rather than uprooting, when an elephant applies pressure to the tree while feeding. However, Viljoen and Bothma (1990a) did not observe elephants breaking down trees and saplings.

The largest tree that appeared to have been broken off by elephants had a 64-cm-diameter stump standing ~1 m. The broken trunk was heavily colonized by shot-borer beetles (Bostrychoidea) and a white-rot fungus, both of which would have weakened the trunk, increasing its susceptibility to breakage. Although high-winds occasionally topple mature *Faidherbia* trees, such events are rare. Only 4 cases were observed during a three-year period in the ephemeral Kuiseb River, all involving large trees (>80 cm) which toppled without breaking. The presence of wood boring beetles and white-rot fungi, in combination with the advanced age of the trees, may have contributed to their collapse (Jacobson, personal observations). No blow-downs or wind-induced breakage of small trees (<40 cm) were observed.

Faidherbia trees broken off at or near ground level by elephants, or with roots damaged by floods, tended to sprout new shoots. These shoots were heavily browsed by elephants and various ungulates. The frequency of root and stump sprouts increased downstream from the Hoanib wetland, reflecting the increased browsing pressure closer to water. No root or stump sprouts were observed within 20 km of the wetland, despite the presence of stumps and damaged trees. Sprouts were present on 22 of 28 (79 %) Faidherbia stumps, 28-36 km downstream, but the sprouts were browsed to within 1-2 cm of their origin. A dramatic increase in both the frequency and the size of root and stump sprouts was observed within the 44-km survey reach (44 km downstream of Dubis), where 79 of 100 damaged Faidherbia exhibited sprouts. Although they were heavily browsed, sprouts ranged from <10 cm to >3 m in height.

The 1995 flood eroded 18 of the 638 (2.8 %) Faidherbia trees measured. Trees were washed out via lateral channel erosion and associated mass wasting of banks, as well as the scour of bed sediments within the active channel. The eroded trees had an average diameter of 80 cm (±37), ranging from 30-190 cm. While many of the trees were washed away, some fell but were held in place by intact roots. These trees, while not killed outright by the floods, were eaten by elephants within three months; branches up to 8 cm in diameter were consumed.

Discussion

While Viljoen and Bothma (1990a) concluded that elephants had no effect on large trees in the Hoanib River from 1963 to 1983, in the twelve years since elephants have radically altered the age structure of the *Faidherbia albida* forest between the Dubis wetland and the terminal floodplain of the Hoanib River. Although the intensity of debarking appears to have increased, the frequency of trees killed via ring-barking has not changed. The low mortality rate associated with ring-barking, observed by Viljoen and

Bothma (1990a) in 1983, and again in the 1995 survey, has also been reported from the Zambezi Valley, where Dunham (1991) recorded only two deaths attributable to ringbarking during an eight-year study of 53 mature trees. In addition, no uprooting of Faidherbia trees was observed in the 1983 (Viljoen and Bothma 1990a) or 1995 surveys in the Hoanib River. Dunham (1989) noted that elephants could not push over healthy Faidherbia albida along the Zambezi River because of their deep roots, although they did occasionally kill trees by ring-barking. Although bark damage does allow the introduction of borer beetles, which may weaken the tree and lead to its collapse (Laws 1970, Anderson and Walker 1974, Barnes 1983a), the low incidence of such infestations (<3 %) in the Hoanib River suggests that this was not a significant factor affecting the size distribution. Thus, it appears that the change in the size distribution within the lower Hoanib River is largely attributable to the selective destruction of small trees (2-20 cm) by elephants.

The effects of such preferential feeding by elephants have been previously noted by Laws (1970), who summarized several studies in Uganda that revealed a marked preference by elephants for small trees, resulting in strongly skewed size distributions. Barnes (1983a) observed a similar pattern in the Ruaha National Park, Tanzania. Severe damage to Faidherbia woodlands has also been reported from Tanzania (Barnes 1983b). Feely (1965) observed that recruitment of Faidherbia albida was severely limited in the Luangwa Valley in Zambia, where the foraging by elephants and various ungulates kept saplings pruned. Finally, Anderson and Walker (1974) observed that old stumps of Acacia tortilis were common along the Sengwa and Lutope Rivers in northern Zimbabwe. The tree was reported to be very susceptible to attack by wood-boring insects; once elephants had stripped some of the bark, it invariably died. Continued pressure from elephants resulted in an uneven age structure along the rivers, as dry season concentrations of browsing animals prevented any significant recruitment of trees. While similar patterns of selective feeding are clearly responsible for the development of a comparatively even-aged stand in the lower Hoanib River, it is unclear what change in conditions occurred between 1983 and 1995 to induce this difference.

The destruction of vegetation by elephants has often been associated with an increase in the local elephant density (Laws 1970, Barnes 1983b). Nonetheless, elephant numbers in the lower Hoanib River have remained relatively stable; surveys from 1982-1995 consistently report approximately 25 animals (Viljoen 1982, Viljoen 1987, Lindeque and Lindeque 1991, personal observations). In addition, no dramatic changes have occurred in the hydrologic or climatic regimes during this period. Rather, it appears that some unknown factor triggered a shift in foraging patterns, resulting in increased foraging pressure on the *Faidherbia* trees within the lower Hoanib River.

Foraging and movement patterns

The seasonal movements and foraging patterns of elephants within the northern Namib Desert were intensively studied by Viljoen in the early 1980's (1989a, 1989b, Viljoen and Bothma 1990b). He recognized the importance of isolated resource patches (i.e., springs and vegetation) to the survival of region's elephants. The riparian vegetation associated with the Hoanib and Hoarusib Rivers was particularly important, both during the dry and wet seasons. Viljoen (1989a) noted that ephemeral river courses and their floodplains, while representing only 3.2 % of the 14,750 km² study area in the northern Namib Desert, provided the only habitat upon which elephants could rely for long-term survival. Similarly, Kerr and Fraser (1975) observed that alluvial plains in the Zambezi Valley, while comprising less than 5 % of their study area, supported roughly 50% of the elephant population during the dry season. They also viewed the maintenance of these areas as essential to the long-term viability of the region's elephant population.

In order to use isolated resource patches, however, elephants must be capable of moving among them. The harsh landscape of the northern Namib Desert provides only isolated respites for any elephant moving across it. Viljoen (1989b) observed that desert-dwelling elephants were well-adapted to the desert and able to go up to four days without drinking water. This ability allowed them to use food resources up to 70 km from water. Not surprisingly, elephants in western Namibia are known to have the largest home ranges of any population studied to date, with estimates of mean home ranges ranging from 2,172 km² (Viljoen 1989b) to ~5,800 km² (Lindeque and Lindeque 1991).

Elephants, both lone bulls and family units, regularly move the ~60 km from the Hoanib floodplain north to the lower Hoarusib River (Viljoen 1989, Lindeque and Lindeque 1991). Lindeque and Lindeque (1991) observed three such movements during eight months study. Viljoen (1989b) observed that elephants rarely traveled more than 20-40 km from water during the dry season, with a mean distance of 25.7 km (sd=13.2) and a maximum of 70 km. This range corresponds with the length of the reach of the lower Hoanib River between the Dubis wetland and the Mudorib confluence, where Faidherbia trees were most severely damaged and the greatest dry season concentration of elephants occurs (Viljoen 1989b).

Following floods, elephants exhibited a strong preference for the Hoanib River floodplain (vlei), where floods trigger an abundance of grasses and forbs. Elephants shifted from a dry season distribution centered around the Dubis wetland area, to a wet season distribution centered on the terminal floodplain, remaining as long as fresh forage was available (Viljoen 1989a). The river course served as a key corridor during these seasonal movements from the Dubis wetland to the floodplain, a distance of ~70 km (Viljoen 1989b). Seasonal movements between a dry season distribution, related to surface water availability, and wet season distribution taking advantage of better food resources, have also been reported from the Tsavo Park (Laws 1970), although these

movements occurred over distances of only 25-40 km. Similar seasonal movement patterns have been reported from the Zambezi Valley in Zimbabwe (Kerr and Fraser 1975).

While isolated habitat patches are of obvious importance to the survival of desert-dwelling elephants, so too are the linking corridors. As Viljoen (1989) observed, critical resource patches are often separated by distances of up to 60 km. In the hyper-arid Namib Desert, any error in navigation between such sites could prove fatal. Thus, the disruption of corridors between key resource patches could have obvious detrimental effects. If access to isolated foraging areas is hindered, pressure on the remaining resource patches within the home range would logically increase, potentially resulting in the over-utilization of accessible patches.

Poaching: the precursor of vegetation change?

Uncontrolled poaching has undoubtedly been the greatest impact on elephants in the northern Namib Desert and has significantly changed their distribution in northwestern Namibia over the past several decades (Viljoen 1987). I hypothesize that poaching induced changes in the movement and foraging patterns of elephants within northwestern Namibia, as has been observed elsewhere in Africa (Caughley 1976, Lewis 1986). However, Viljoen (1989b) recorded no cases of elephants moving into new ranges as a result of hunting or other pressures. While elephants moved extensively within large home ranges, fidelity to these ranges was high, even when animals suffered heavy hunting pressures (Viljoen 1987). Viljoen (1989b) noted that this conflicted with the 'compression hypothesis' (Caughley 1976), which has been used to explain mass shifts of elephant populations due to human pressure. The 'compression hypothesis' suggests that elephants are driven into sanctuary areas by increasing levels of disturbance, resulting in localized concentrations that may seriously damage vegetative communities (Caughley 1976). It is also possible, however, that elephants losing only part of their home range to human activity may be 'compressed' into the remainder, as was noted by Viljoen (1989).

'Compression' need not imply only a shift in distribution and an associated change in density, but could also be applied to situations where disturbances force animals to avoid localized portions of their normal range, and spend more time foraging in disturbance-free areas. Such shifts might be too subtle to be perceived as an alteration in elephant distribution or density across a landscape. Yet, such shifts could affect resource utilization patterns within the northern Namib Desert. If, for example, a key habitat patch is lost, animals would be forced to restrict their activity to the remaining patches. The density of animals within any given patch would not necessarily increase, but use of some patches could become excessive. Viljoen (1989) noted the reluctance of elephants to move into new areas within western Namibia, which might act to increase the probability of the 'home range compression' previously described. While admittedly speculative, such a

scenario may explain the significant habitat alterations that have occurred within the lower Hoanib River.

Similar effects have been observed in the Luangwa Valley in Zambia, where poaching induced changes in food preferences and range patterns of elephants (Lewis 1986). These changes restricted food availability, resulting in a decline in the region's woodland. Lewis noted that the increased browsing pressure was the result of altered feeding behaviors (i.e., time spent within particular habitat patches) rather than increased elephant density (Caughley 1976). Elephants in the Luangwa Valley rapidly returned (within 1-2 years) to former foraging areas once anthropogenic disturbances were controlled (Lewis 1986).

It is unclear, however, whether the human disturbances, particularly poaching, induced such shifts in the patterns of resource utilization within elephant home ranges in the Namib. Intensive studies of the distribution and movements of individual elephants and family units only began in October 1980 (Viljoen 1989b). By this time, significant disturbances had already occurred throughout the study area, including hunting (Viljoen 1987). In fact, Viljoen's study period, from October 1980 to January 1983 coincided with intensive poaching and other disturbances. From July 1979-July 1982, a total of 121 elephants were killed within northwestern Namibia, some 35% of the total population (Viljoen 1982).

An aerial census in 1982 revealed the extent of the poaching which was occurring in the immediate vicinity of the Hoanib River and its tributaries (Viljoen 1982): While 25 elephants were observed within the Hoanib River west of Sesfontein, 11 carcasses were also seen. To the north, zero live and 11 dead were observed in the Hoarusib River; to the south, zero live and 6 dead on the Kharokhaob Plain; to the east, 11 live and 18 dead on the Khowarib Plain; and upstream of the Khowarib Canyon, 38 live and 41 dead. Ground surveys confirmed that 90 % had been shot within the past three years (Viljoen 1982). No observations of movement patterns were made before the poaching, however, obstructing any attempt to assess whether poaching triggered shifts in foraging patterns.

An uncertain future

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The future of the forest, the elephants, and the river itself, is uncertain. A wide range of development plans have been proposed for the Hoanib River, with particular emphasis upon expanded agricultural activities that rely upon the water resources of the Hoanib River (MAWRD 1994). Ground-water pumping of the alluvial aquifer of the Hoanib River, between Khowarib and Anabeb, and construction of a dam in the Khowarib Canyon, are two options for agricultural development. Either option will likely have serious impacts upon the lower Hoanib River ecosystem. A reduction in flood frequency or extensive groundwater pumping would lower the water table within the lower Hoanib River, having multiple effects upon the region's biota.

Hydrologic alterations could lead to the desiccation of the Dubis wetland, a critical dry-season resource for the region's elephants, and trigger the senescence of the even-aged Faidherbia forest along the lower river. Young and Lindsay (1988) noted that environmental stressors may act to trigger synchronous die-offs within even-aged stands. Such a die-off occurred in the lower Kuiseb River during the early 1980's when 4 years without floods triggered the collapse of large Faidherbia albida trees (Ward and Breen 1983). A similar die-off occurred within the lower Swakop River, along with the desiccation of wetlands, in response to hydrologic alterations induced by an upstream impoundment (Jacobson et al. 1995).

Avoiding such dramatic changes is contingent upon the maintenance of key ecological processes, particularly flooding, critical to the maintenance of the elephant's principal resource patches (i.e., springs and vegetation). Floods in ephemeral rivers act to decouple elephants from fluctuations in the harsh local climate. Although local rainfall may differ by more than 100 % among years, mean daily movements of elephants may remain unchanged, as floods originating in the upper catchment provide water and stimulate vegetation growth along the rivers and their floodplains (Viljoen 1989b).

If the Faidherbia forest within the lower Hoanib River is to recover, the browsing pressure and associated destruction of young trees must decrease. Eastward extensions of the elephants' range could provide an outlet to reduce pressure on the river's vegetation, although they could also lead to increased conflicts with humans. Prior to the heavy poaching of the 1970's and early 1980's, Owen-Smith (1971) observed that elephants ranged from the Hoanib River west of Sesfontein across the Khowarib Plains, and drank at Anabeb and from small springs in the mountains south of Warmquelle and Sesfontein. An aerial census in 1975 counted only five elephants in the Hoanib River west of Sesfontein but 33 on the plains to the south (Viljoen 1987). An elephant traveling upstream from the Dubis wetland could reach Sesfontein in ~30 km, Anabeb in ~45 km, and the Khowarib canyon in ~70 km. Moving southeast through the mountains, elephants could reach the canyon in ~50 km. Such movements would significantly increase access to vegetation resources, relative to those currently utilized in the vicinity of the lower Hoanib River. While it remains to be seen if such movements will occur, their probability will increase in response to further declines in resource availability in the lower reaches of the river. This would be particularly true in the event of any significant alterations of the river's surface or subsurface hydrologic regimes. At present, uncoordinated land use within the region leaves the future of the lower Hoanib River and its natural resources uncertain.

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