

Status and Action Plan for the Plains Zebra (*Equus burchellii*)

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4.1 Nomenclature and conservation status

Scientific name:

Equus burchellii Gray
Equus burchellii boehmi
Equus burchellii zambesiansis
Equus burchellii crawshayi
Equus burchellii chapmani
Equus burchellii antiquorum
Equus burchellii burchellii

Important synonyms:

Asinus burchellii Gray 1825
Equus burchellii Smuts 1832
Hippotigris burchelli Smith 1841
Equus quagga burchelli Pocock 1904

Common names:

Plains zebra, common zebra, Burchell's zebra, painted quagga

Indigenous names:

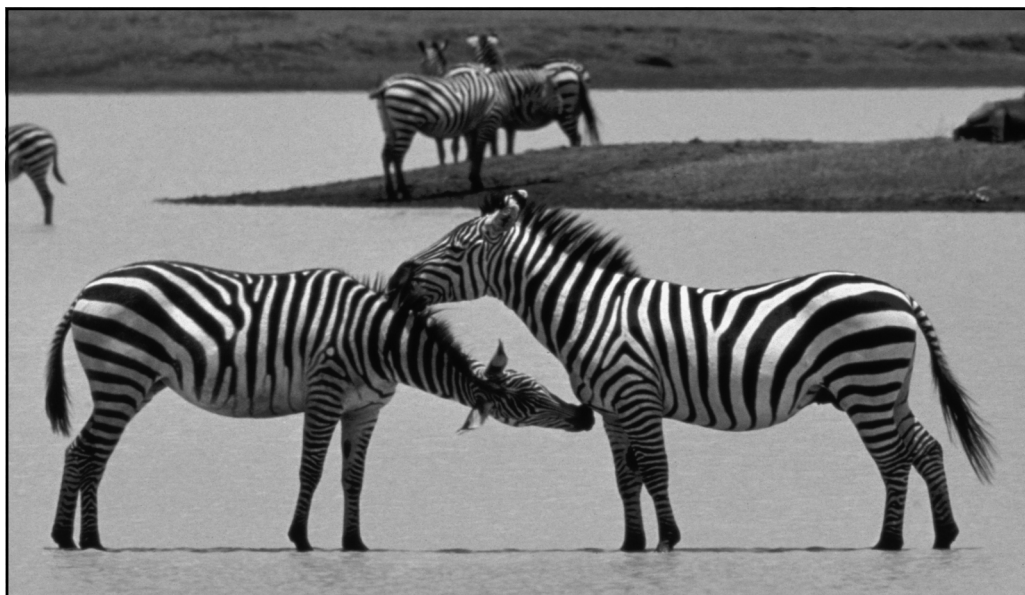
Punda milia (Kiswahili), itiko (Kichagga), eutulege (Luganda, Runyoro), etuko (Karamojong), lagwar (Lwo),

entorege (Runyankore), injiga (Ishinyika), hares (Kiliangulu), eloidigo (Maasai), iqwaha (Xhosa), idube (Zulu, Ndebele), mangwa (Tsonga), pitsi (Sotho, Tswana), mbidi (Venda), mbizi (Karanga), bontsebra or bontkwagga (Afrikaans)

IUCN Red List Category (*E. burchellii*, *E.b. antiquorum*, and *E.b. boehmi* were assessed using version 3.1; all others with version 2.3):

Equus burchellii **LC** Least Concern
E. b. boehmi **LR** Lower Risk
E. b. zambesiansis **DD** Data Deficient (? extinct in wild)
E. b. crawshayi **DD** Data Deficient (? endangered)
E. b. chapmani **DD** Data Deficient
E. b. antiquorum **LR** Lower Risk
E. b. burchellii **EX** Extinct (1930)

As recently as 15 years ago, the plains zebra could be found in nearly all the countries of eastern, southern, and south-western Africa. It has since been extirpated from several parts of this range, although it remains the most widespread and abundant equid in the world today. Where the plains zebra still occurs, it is usually a numerically dominant member of the ungulate community and therefore plays an important role in the overall dynamics and welfare of its



The plains zebra (*Equus burchellii*).

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grassland habitat. The primary threats to this species include overhunting and loss of habitat to human development and livestock ranching. Overall, those populations constituting a major proportion of the species' total global population have remained stable over the past ten years, or have only recently begun to decline. However, because nearly 70% of the global population resides in only two countries – Kenya and Tanzania – the long-term preservation of the species in a wild, free-ranging state depends critically on their fate in this region of East Africa.

4.2 Taxonomy

A genetics-based taxonomy of the plains zebra has not been fully resolved and there is a troubling lack of consensus among the many traditional taxonomies put forward for this species (Cabrera 1936; Roberts 1951; Sidney 1965; Groves 1974; Kingdon 1979; Skinner and Smithers 1990; Groves' chapter in this document). For the purposes of this report, we follow Duncan's lead in the preceding Action Plan (1992a) and consider the species to consist of six subspecies: Grant's (*Equus b. boehmi*), Crawshay's (*E. b. crawshayi*), Upper Zambezi (*E. b. zambeziensis*), Chapman's (*E. b. chapmani*), Damara (*E. b. antiquorum*), and the nominate Burchell's (*E. b. burchellii*). Whether ultimately judged to be accurate or not, we use these historical subspecies designations because (i) they are convenient for summarising regional differences in population trends and their causes, (ii) they correspond with consistent morphological differences, and (iii) they may yet be important to plains zebra conservation if the genetic distinctions among them are sizeable enough to merit preservation.

Current plains zebra taxonomies divide the species' range into contiguous units, each home to a morphologically distinct subspecies (Figure 4.1). The most conspicuous morphological differences include body size and the width, intensity, and coverage of dark stripes on the adult pelage. In general, the extent of stripe coverage decreases as one moves from north to south, although variation in stripe patterns within any particular population can be large and even include variants more characteristic of other subspecies (see Kingdon 1979). Body size follows a similar north-south cline, with *E. b. antiquorum* in the south averaging 28–40% larger than *E. b. grantii* in the north (Smuts 1975). Small differences in tooth and cranial characters also separate some subspecies (Groves 1974; Groves and Willoughby 1981).

Genetic differences presumably account for these morphological distinctions among subspecies yet it is under debate as to whether subspecific boundaries delineate genetically unique breeding populations or, alternatively, divide a continuum of genetic variation into somewhat arbitrary segments. Evidence derived from analysis of

mitochondrial DNA favors the latter hypothesis since it suggests that genetic differentiation across the species' range is simply clinal and changes smoothly as a function of distance (N. Georgiadis unpublished data; A. Oakenfull unpublished data). However, this result appears at odds with one of the few points of consensus among traditional taxonomists, who perceive geographic features that are likely to inhibit dispersal, most notably the Zambezi River (Figure 4.1), as important boundaries between subspecies (Roberts 1951; Sidney 1965; Groves 1974; Kingdon 1979; Skinner and Smithers 1990). These features may impede gene flow sufficiently to maintain morphologically distinct and locally adapted subspecies without generating the complete barriers to reproduction and dispersal that lead to speciation. More thorough sampling of populations throughout the species' range is needed if we are to resolve the taxonomy of the plains zebra from genetic information. Samples from populations in the middle of the species' range (e.g. Zambia, Zimbabwe, Malawi, and Mozambique) and at its margins (e.g. Namibia, Angola, Sudan, and Somalia) would be particularly valuable.

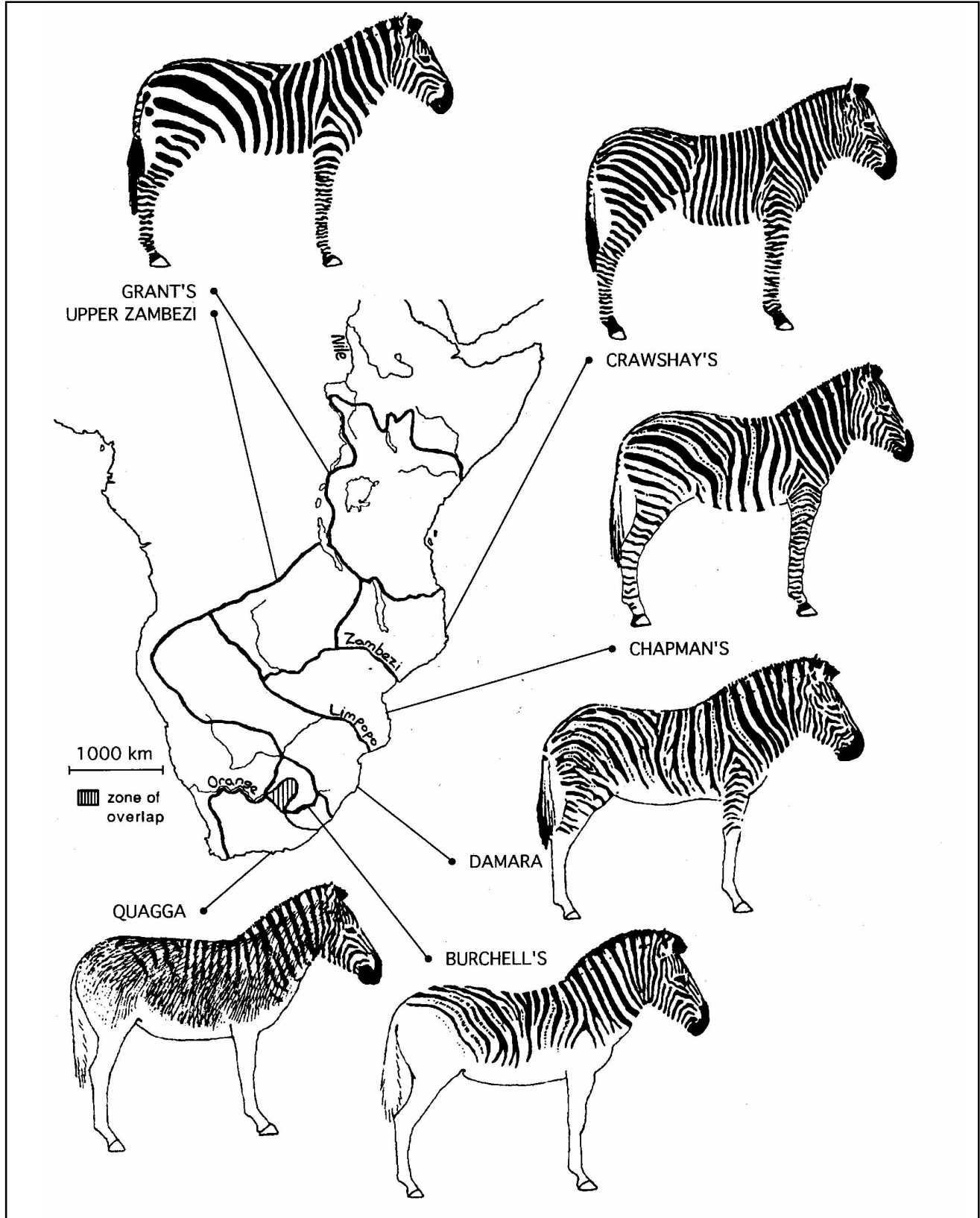
4.3 Quagga: species or subspecies?

The quagga (*E. b. quagga*) represents a possible seventh subspecies of plains zebra if one accepts the results of recent mitochondrial DNA and immunological analyses (Higuchi *et al.* 1984; Lowenstein and Ryder 1985; George and Ryder 1986). These studies have used dried tissue from 19th century museum specimens to demonstrate a greater affinity between the quagga and the plains zebra than that between the quagga and a neighbouring species, the mountain zebra (*E. zebra*). Unfortunately, the genetic analysis, in particular, was based on a very small sample of base pairs, or <2% of that used to resolve analogous differences among the other equid species. Other evidence, including a distinctive stripe pattern (Figure 4.1) and slight tooth and cranial differences on par with those seen between the plains and mountain zebras, suggests a separate species designation should be given for the quagga (Cabrera 1936; Groves 1974; Bennett 1980).

The heart of the quagga's range was the semi-arid and temperate Karroo in southernmost Africa, an area of unique ecology and high floral and faunal endemism. Anecdotal accounts indicate that quaggas and Burchell's zebra encountered each other in a narrow zone of range overlap north of the Orange River (Figure 4.1) – in contrast to the non-overlapping ranges of the other plains zebra subspecies – but they did not appear to interbreed (see citations in Sidney 1965; Groves 1974; Kingdon 1979). Unfortunately, we may never know the quagga's true taxonomic relationship to the other plains zebras because both the quagga and the Burchell's subspecies were driven to extinction in the late 19th and early 20th centuries,

Figure 4.1. Historical range (c. 1800) for each plains zebra subspecies and the quagga (*E. quagga*).

From north to south, note the change in stripe width, presence of shadow striping, and the extent of stripe coverage on the legs, rump, and flanks. Subspecies: Grant's (*Equus b. boehmi*), Crawshay's (*E. b. crawshayi*), Upper Zambezi (*E. b. zambeziensis*), Chapman's (*E. b. chapmanni*), Damara (*E. b. antiquorum*), Burchell's (*E. b. burchellii*). (Adapted from Groves 1974 and Kingdon 1979.)



respectively, by overhunting and competition with livestock, primarily sheep. A recently initiated captive-breeding programme is attempting to 'resurrect' the quagga by breeding individuals with quagga-like stripe patterns from stock of the Damara subspecies (Harley 1988). (N.B. Those who consider the quagga a seventh subspecies prefer to name this plains zebra species *E. quagga* in place of *E. burchellii*.)

4.4 Range

At the beginning of the 19th century, and prior to the extensive European colonisation of sub-Saharan Africa, the plains zebra ranged throughout most of the eastern, southern, and south-western regions of the continent (Figure 4.2). Although this species may have occurred as far north as Algeria during the Neolithic period (Groves 1974), by the 1800s none were found further north than southern Ethiopia and southern Sudan, east of the Nile River (Sidney 1965; Groves 1974; Kingdon 1979). The core of the historical range included what is now Kenya, Tanzania, and Sudan – with peripheral populations in Somalia, Uganda, Burundi, and Rwanda – and continued south through Malawi, Mozambique, Zambia, Zimbabwe, northern and eastern

Botswana, Swaziland, Lesotho, and South Africa as far south as the Orange River. Plains zebra were also historically found in the south-eastern Democratic Republic of Congo (formerly Zaire), and extended westward and south through southern Angola and northern Namibia. As detailed below, this species is now extinct in two countries – Burundi and Lesotho – and may have been extirpated within the last ten years from Angola.

4.5 Ecology: what drives habitat selection and ranging patterns?

Plains zebra graze almost exclusively and are therefore strongly associated with grasslands and savanna woodlands, but they can be found in these habitats in both tropical and temperate climates, and from sea level to over 3,500m in elevation. Only deserts, dense forests, and permanent wetlands are avoided. Adults need to drink at least once per day – lactating females may require two daily trips to water – limiting their range to the close vicinity (five to ten kilometres) of reliable water sources. Many populations are seasonally migratory, travelling hundreds of kilometres annually to track vegetational flushes caused by rainfall (e.g. Serengeti-Masai Mara ecosystem: Maddock 1979).

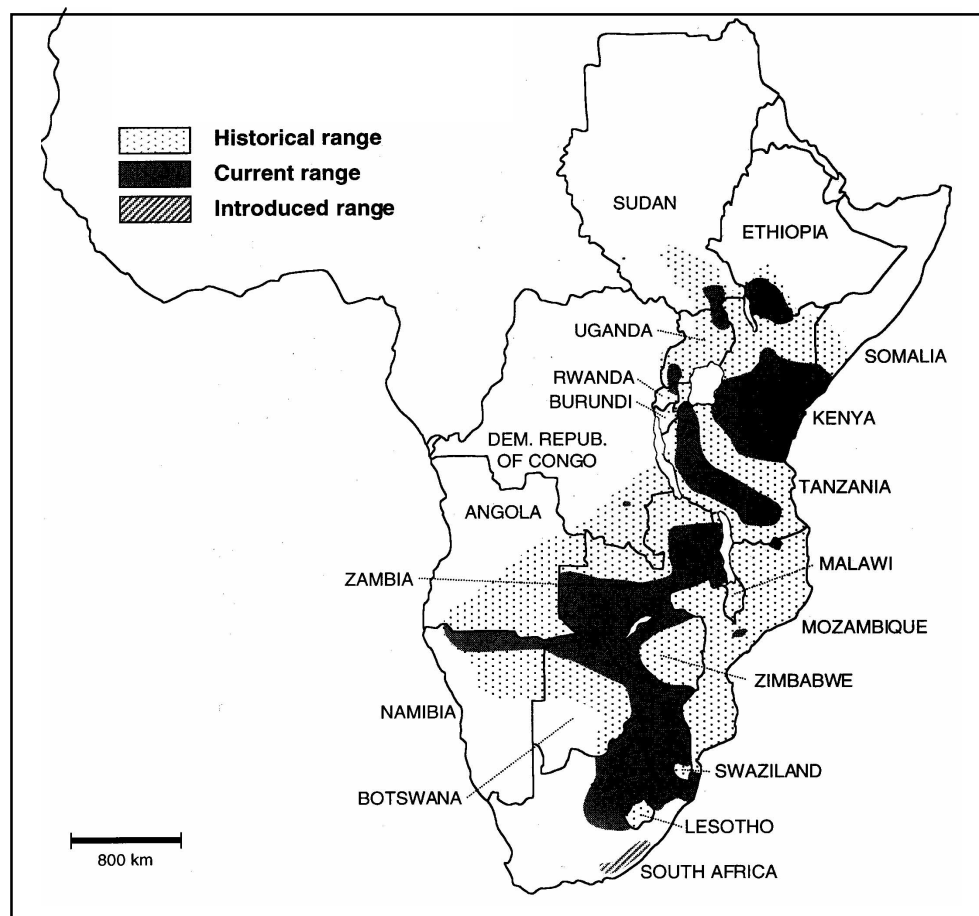


Figure 4.2. The historical and current ranges of the plains zebra. Note the modern introduction of the species in south-eastern South Africa.

(For a breakdown of subspecies population sizes by country, refer to Table 4.3.)

However, even in regions where the majority of individuals migrate, some individuals usually remain as year-round residents. Thus, population density in an area may fluctuate by two or three orders of magnitude (e.g. from 0.01 to 11 per km² on the Simanjiro Plains in Tanzania: Kahurananga 1981). What distinguishes migratory from resident populations is an interesting question for further study, but it is most likely influenced by the frequency-dependent nature of resource availability.

4.6 Ecology: promoter of grassland biodiversity

In contrast to the antelopes and other ruminants that comprise the main consumers of grass on the African savannas, plains zebra utilise a hind-gut digestive system that allows them to process their food at relatively faster rates. Consequently, coarse vegetation of low nutritional value can sustain zebras as long as it is abundant, whereas similarly sized ruminants would starve on the same diet (Duncan 1992b). This critical difference in digestive systems has at least three important implications. First, by being able to exploit a greater range in grass quality, plains zebra occupy a more extensive geographical range, a larger variety of habitats, and reach higher densities in some of the poorest grasslands than most other ruminants of equivalent size. Second, this ability to subsist on low quality forage, when combined with relatively large body size and its concomitant lowering of transport costs, enables plains zebra to undergo large migrations to track changing resources. Thirdly, plains zebra typically move into a grassland ahead of other grazers and, by removing the older growth layer of lignified stems, sheaths, and seed heads, open it up to grazing by the more selective ruminants, such as wildebeest and Thompson's gazelle, which concentrate on the tender and nutritious new growth (Owaga 1975). Thus, on the Serengeti Plains and elsewhere, plains zebra play a key role in initiating the pattern of succession within the grazer community, thereby enriching the variety and numbers of herbivores that these grasslands sustain (Bell 1971).

4.7 Population dynamics: important parameters and ecological consequences

Despite the fact that zebras are the most abundant and most visible of all African grazing mammals, the dynamics of specific populations are poorly documented. Descriptions of population trajectories are often noted and typically compared with those of other sympatric grazing species, but they reveal little about the mechanisms controlling these trends and offer few insights into

predicting what lies ahead. It was observed, for example, that during the 1960s and 1970s zebra numbers in the Serengeti remained relatively constant while those of wildebeest and buffalo increased dramatically, suggesting that the dynamics of zebra populations were being governed differently from those of its competitors. During this period it was also noted that diseases affecting ungulates were absent and that vegetation levels had increased steadily. To explain these differing responses, an intriguing hypothesis was proposed: whereas wildebeest and buffalo numbers were controlled by vegetation abundance and competition for food, zebras numbers were being limited by predators (Sinclair and Norton-Griffiths 1982; Senzota 1988). A similar study of ungulate population trends in Namibia's Etosha National Park reached the same conclusion, citing predation and possibly disease (anthrax) as more important regulators of plains zebra numbers than food abundance (Gasaway *et al.* 1996). Unfortunately, in both studies, the detailed demographic measures that could determine the extent to which population processes are governed by 'bottom-up' or 'top-down' mechanisms are lacking.

As Table 4.1 shows, several populations have been surveyed and censused, but key life-history variables, especially with respect to vital demographic rates, are often not recorded. Overall, plains zebra breeding groups are of moderate size with each male associating with two to three females and their recent offspring. But even as these few studies show, measures of harem size and composition vary among study sites by a factor of two. With respect to demographic characteristics and vital rates, interpopulation variation is even greater. Doubtless this is the result of marked seasonal and yearly fluctuations in environmental conditions, which are known to have major impacts on patterns of foal survival, adult sex ratio, and population density.

As yet, few studies have recorded these trends for long enough to allow us to measure the sensitivity of these variables to changing environmental conditions. As illustrated in Table 4.2, Ngorongoro zebra exhibit yearly variation. The fraction of females giving birth during consecutive years increased from 38% in 1987 to 46% in 1988, while the male:female sex ratio among foals dropped from 1.3 in 1987 to 1.1 in 1988. At this point, however, it is too early to tell whether this level of variation is biologically significant. Moreover, longer term studies will be needed to determine if any systematic correlations can be detected among demographic variables. From studies on Asiatic asses, *E. hemionus*, by Saltz and Rubenstein (1995), we know that identifying these associations is critical to understanding the processes that shape the reproductive potential, and hence recruitment capabilities, of a population. In this closely related species, female age, presumably a good indicator of bodily condition, affects the sex of a female's foal: primiparous

Table 4.1. Summary of demographic variables for plains zebra populations throughout the species' range.

Site	Harem Size (inclu. 1 stallion/)				Recruitment		Mortality Rate		Adult Sex Ratio Males/Females	Source ¹
	Total Harem (mean)	(max.)	Adult Females (mean)	(max.)	%Foals (=1 yr.)	%Juveniles (1<X=3 yrs.)	1st year	Adult		
Kenya										
Samburu NP, Athi-Kapiti Plains	8.2	14	4.7	6	0.20 0.26	0.12 0.28	0.33 0.38	0.17	0.62	1, 2 3
Tanzania										
Ngorongoro Crater	7.7	16	2.8	6		0.20	0.19	0.03–0.09		4, 5
	5.0	10	2.5	6	0.19	0.19	0.19	0.07	0.69–0.88	6
Loliondo area									0.56	7
Serengeti NP	5.1	11	2.2	5	0.11		0.30	0.11		4, 8
Rukwa area	5.4	10	2.5	6						9
Malawi										
Nyika NP					0.10				1.00	10
Zimbabwe										
Wankie NP	4.6	8	2.6	5						4
Namibia										
Etosha NP	4.7	9	2.3	5		0.18				4, 11
South Africa										
Kruger NP	4.5	8	2.4	4		0.09				4, 11
	4.2	11			0.12	0.06	0.47	0.03–0.13	0.75	12, 13

¹ – References cited: (1) Rubenstein 1989; (2) Ohsawa 1982; (3) Petersen and Casebeer 1972; (4) Klingel 1969; (5) Klingel 1975; (6) Hack and Rubenstein, unpublished data; (7) Skoog in Smuts 1976a; (8) Sinclair and Norton-Griffiths 1982; (9) Klingel 1967; (10) Munthali and Banda 1992; (11) Gasaway *et al.* 1996; (12) Smuts 1976a; (13) Smuts 1976b.

¹ – References cited: (1) Rubenstein 1989; (2) Ohsawa 1982; (3) Petersen and Casebeer 1972; (4) Klingel 1969; (5) Klingel 1975; (6) Hack and Rubenstein, unpublished data; (7) Skoog in Smuts 1976a; (8) Sinclair and Norton-Griffiths 1982; (9) Klingel 1967; (10) Munthali and Banda 1992; (11) Gasaway *et al.* 1996; (12) Smuts 1976a; (13) Smuts 1976b.

and old females give birth mostly to daughters, while prime-aged females have mostly sons. The implication of this pattern is clear. If plains zebras behave like their close kin, then knowing that such correlations between variables exist will affect the successful management of any population actively being poached, legally cropped, or being created by the release of translocated animals.

Comprehensive data of the types presented are essential for making reliable assessments of a population's status, as well as for designing and implementing management plans, but by themselves they are not sufficient to do either. In addition, age-specific, or at least stage-specific, vital rates are needed. Unfortunately, few such data exist. Only one life table for the plains zebra has been compiled (Petersen and Casebeer 1972) and cursory analysis by simulation (Senzota 1988) suggested that the Kenyan

population it depicts has a stable age structure. It is unlikely, however, that this age distribution will be representative of all zebra populations given the highly variable nature of the demographic variables listed above (Tables 4.1 and 4.2). Demographic profiles from other studies are even less informative, being derived from age-specific census sightings and samples of serendipitously collected skulls and carcasses (e.g. Smuts 1976). Such data can only provide age-sex distributions that are crude approximations of the actual age structure.

Apart from providing a quantitative description of a population's state, actual age-specific life history measures, especially vital rates, are essential if population projections or viability analyses are to be performed. Clearly, more data are needed before appropriate management or conservation strategies are instituted, but if the Kenyan population's (Petersen and Casebeer 1972) age-specific survival and fecundity patterns are representative, then the patterns that emerge from employing them in population projection simulations can be instructive. When stochastic Leslie matrix population projection models incorporating density-dependence (e.g. Dobson and Lyles 1989; Rubenstein and Dobson 1996) are applied to populations characterised by Athi Plains' vital rates, plains zebra populations facing natural levels of predation and inhabiting stable landscapes that are minimally impacted by people (e.g. East African national parks and other unfenced protected areas) tend to reach equilibrium and remain stable for decades. Even populations inhabiting unprotected areas that are divided into large ranches, such as in the Laikipia region of central Kenya which

Table 4.2. Summary of plains zebra demographic parameters from a free-ranging population of known individuals inhabiting Ngorongoro Crater, Tanzania.

	1987	1988
Females with foals (Jan–Aug)	37.6% (n=210)	46.0% (n=274)
Foal survivorship in 1st year	(n=93)	80.6%
Foal sex ratio (male/female)	1.29	1.11
Yearling sex ratio	-	1.50
Female fecundity:		
No foal either year	-	28.1%
One foal over two years	-	61.0%
Two foals over two years	-	10.9%

covers over 7,000km² and receives nearly 600mm of rainfall per year, are also likely to remain stable as long as no major changes in land use occur.

Results of the model show that the current Laikipia population of approximately 25,000 adults will oscillate around an average of 23,000 adults over the next 30 years. Simulations also reveal that the population will increase slowly if further reductions in predators occur or if global climate change leads to rainfall increases of approximately 20%. But what is perhaps most interesting is that the Laikipia population will remain stable under a variety of moderate cropping regimes. Adult numbers will indeed be lowered by repeated cropping – either by design or by poaching – but they will tend to hover at 20,000 if cropping is limited to removing either 15% of only the young males (aged two to five) or five percent of the entire population, indiscriminately chosen, on a yearly basis. The most successful strategy will depend on other factors and trade-offs that often determine the shape of a multiple land-use scheme. However, only by knowing the life-history details of a population does it become possible to model population processes so that alternative management and conservation strategies can be evaluated and compared. For these scenarios to be accurate, and hence their predictions meaningful, reliable estimates of age-specific demographic vital rates are required. And at the moment, such data are usually absent.

4.8 Social organisation: implications for population dynamics and genetics

Plains zebra are highly social animals. Like the mountain zebra and horse, the basic unit in plains zebra society is the ‘harem’, consisting of a single adult male, one to six adult females, and both sexes of offspring up to the age of two to three years (Klingel 1969; Rubenstein 1986). Females may remain together in the same harem for much of their reproductive lives, and the harem male defends his exclusive right to mate with them. Unlike other mammalian societies based on cohesive, long-lasting female groups, such as those of lions and elephants, the females in an equid harem are not genetically related; both sexes of offspring disperse from their natal group. Males without harems – including young males that have recently dispersed from their natal harems and older males that are unable to compete successfully or have lost their harems to rivals – live as ‘bachelors’ in loose aggregations that may number as many as 50 individuals. Both harems and bachelor groups come together to form larger herds when grazing, sleeping, or moving between areas. This multileveled social organisation is more characteristic of primates, such as baboons, than it is of ungulates, yet why plains zebra form such societies is not fully known and currently under study (Hack and Rubenstein, in prep.).

The plains zebra’s unusual social organisation has several implications for the population dynamics and genetics of this species. Evidence from studies of other harem-forming equids, such as feral horses, suggests that social instability, particularly a high rate of turnover among harem males, adversely affects female reproductive success and patterns of age-specific fecundity (Berger 1983; Rubenstein unpublished data). The increased levels of sexual harassment that result can lower female body condition and disrupt normal endocrine function. A similar linkage between social stability and recruitment probably exists in plains zebra, highlighting an important demographic factor to consider in harvesting strategies since the killing of males is often favoured.

The unusual structure of plains zebra populations also has implications for the conservation of genetic diversity. Polygyny, male tenures as long as ten years (Hack and Rubenstein, unpublished data), together with a high bachelor mortality rate indicate that some males will never have the opportunity to breed. Thus, effective or genetic population sizes will often be substantially less than adult census population sizes. On the other hand, the reduction in effective population size will be less than that for other group-living ungulates because females within each plains zebra breeding group are not genetically related. As a result, founder populations of a few harems will have relatively high genetic diversity. This is particularly relevant for reintroduction efforts since it implies that a normal social structure, and the social stability and reproductive benefits it confers, does not have to be traded off against the selection of individuals to ensure sufficient genetic diversity for the long-term health of a population.

4.9 Current population numbers and trends

Based on information presented in this report, the total global population of plains zebra in the wild is 663,212, or roughly equal to that estimated by Duncan in the last Action Plan (1992a) despite the present survey’s more thorough coverage (Appendix 3). Most of the data used to arrive at this estimate are from censuses conducted within the past seven years. Countries for which no recent data are available probably harbour less than three percent of the total global population. Because much of the data used in this survey derive from aerial sample counts, which inherently miss an unknown proportion of animals, the total population size reported is almost certainly an underestimate of the actual population size. Application of a suitable correction factor, typically between 1.2 and 2.0 for conspicuous savanna ungulates like the plains zebra, places the actual worldwide population between 796,000 and 1,326,000 individuals.

Table 4.3. Summary of plains zebra population sizes per country, and percentages held per country for both the global and subspecific totals.

	Total population per country	% of subspecies' total population	% of species' total population
Grant's total	496,703		
Tanzania	296,508	59.7	44.7
Kenya	152,490	30.7	23.0
Sudan	33,050	6.7	5.0
Ethiopia	7,470	1.5	1.1
Uganda	3,137	0.6	0.5
Somalia	1,000?	0.2	0.2
Burundi	extinct		
Rwanda	3,048		
Upper Zambezi total	19,219		
Zambia	18,219	94.8	2.7
Dem. Rep. Congo (Zaire)	<1000	5.2	0.2
Angola	extinct?		
Crawshaw's total	23,020		
Zambia	21,250	92.3	3.2
Malawi	670	2.9	0.1
Mozambique	1,100	4.8	0.2
Chapman's total	20,294		
Mozambique	65	0.3	0.0
Zimbabwe	20,135	99.2	3.0
Botswana	94	0.5	0.0
Damara total	103,976		
Botswana	34,200	32.9	5.2
Namibia	13,090	12.6	2.0
Swaziland	1,000	1.0	0.2
Lesotho	extinct		
South Africa	55,686	53.6	8.4
Species total	663,212		

The plains zebra is not currently listed in either CITES Appendix I or II. Applying the IUCN Red List of Threatened Animals criteria for threatened species (IUCN 1994) results in a designation of Lower Risk, Conservation Dependent for the species. Although no one subspecies has yet reached the criteria for being deemed Vulnerable, two would certainly become Vulnerable if conservation programmes in Zambia, which protect the plains zebra and other wildlife, were dismantled (Table 4.3).

Over 75% of the world's plains zebra are of the Grant's subspecies and, of these, nearly three-quarters live in just two countries – Tanzania and Kenya (Figure 4.3, Table 4.3). Both countries have extensive national park and reserve systems with well-developed wildlife monitoring programmes, and they derive substantial income from wildlife-based tourism. Global recognition of the importance of this region's wildlife and the countries' commitments to wildlife conservation demonstrated by their governments have attracted significant and vital international support for establishing and sustaining protected areas.

In Tanzania, national parks, game reserves, game-controlled areas and other protected lands cover approximately 25% of the country. Of these, the Serengeti

National Park in the north supports the world's single largest plains zebra population (151,000), as many as a third of which migrate seasonally into south-western Kenya. The Serengeti population has been relatively stable over the past 30 years, but recently appears to be decreasing due to human encroachment and illegal hunting for meat (Campbell and Borner 1995). The estimated annual off-take of 12.9% (Hofer *et al.* 1996) is unlikely to be sustainable given what we currently know about the demography of this species (Tables 4.1 and 4.2). Most other protected populations in Tanzania are stable, although some, such as those of Tarangire National Park in the north and the Burigi-Biharamulo ecosystem in the north-west, depend heavily on unprotected lands for much of their annual migratory cycles. Current agricultural expansion in these unprotected areas is likely to cause future population declines. Improved wildlife protection and management in the southern Selous ecosystem have caused its substantial plains zebra population, the third largest in the country, to increase over the last ten years. Plains zebra numbers in the western Katavi-Rukwa ecosystem have similarly increased.

It is important to note that large tracts of land in Tanzania are not currently censused for wildlife. Many

certainly contain plains zebra populations, though at presumably low densities due to legal and illegal hunting. Consideration of these uncensused populations could significantly increase the estimated total population for the country.

Kenya's plains zebra reside in 13 regularly censused rangeland districts, four of which support over 80% of the country's total population. Several national parks and reserves (e.g. Tsavo, Masai Mara) harbour important resident populations or are vital dry season refuges (e.g. Amboseli, Nairobi). However, in total, protected lands support less than 10% of the country's plains zebra population (Grunblatt *et al.* 1995). Thus, the long-term fate of this species in Kenya depends critically on their success in unprotected areas. Since 1977, most rangeland ungulates have declined in abundance by 40–80% with the apparent exception of one species, the plains zebra (Grunblatt *et al.* 1996). Unfortunately, a country-wide increase of 13% in plains zebra numbers, fuelled by growing populations in just four districts, masks declines averaging 45% everywhere else. Agricultural expansion and competition with livestock constitute the most important pressures on plains zebra populations, particularly in the south. Legal harvesting of plains zebra for meat and skins

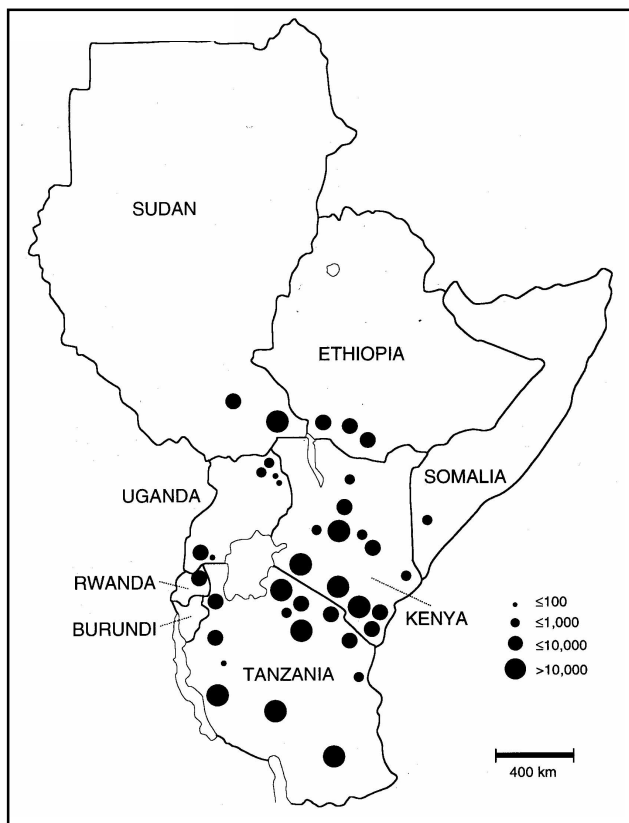
currently occurs in several rangeland areas (e.g. Laikipia), and Kenya may soon join the rest of eastern and southern Africa in allowing trophy hunting of this and other species.

Elsewhere throughout its range the Grant's subspecies has not fared as well (Figures 4.2 and 4.3; Table 4.3). Recent civil wars in Rwanda, Somalia, Sudan, Ethiopia, and Uganda have caused dramatic declines in all wildlife populations, including those of Grant's zebra. In all cases, an abundance of weaponry and the erosion of the wildlife protection infrastructure have led to severe overhunting for meat and intensified encroachment by humans and their livestock. In densely populated Rwanda, plains zebra were already confined to a single national park (Akagera) and neighbouring reserve in the north-east prior to the outbreak of civil war in the early 1990s. Since then, these areas have been intensively hunted and over-run with refugees and their livestock to the extent that much of the park was recently de-gazetted. Ungulate populations in the region have generally suffered 80% declines since 1990, but plains zebra still occur and appear to have only declined by 20% during this same period. Zebra are apparently considered less palatable than other ungulates in Rwanda and may be better at avoiding humans, accounting for their less steep decline (Williams and Ntayombya 1999). Southern Somalia may still have a small, but viable plains zebra population (Estes 1995). Southern Sudan probably retains significant numbers of plains zebra, since it had the third largest population of Grant's in 1983, but we have no current data for this country. Efforts to resurvey the Boma and Southern National Parks are currently underway (R. Olivier *in litt.* 8/97). Ethiopia's plains zebra have rebounded in some areas, primarily the south-western lowlands, from almost catastrophic declines during the 1970s and 1980s. However, levels of wildlife management and protection remain low due to a lack of resources and little public awareness of the value of wildlife. Increasing poaching and human encroachment on protected lands are likely to erase these gains in the near future (C. Schloeder *in litt.* 8/96; Graham *et al.* 1996).

Civil strife in Uganda during the 1970s and 1980s resulted in the devastation of many wildlife populations despite a well-developed system of conservation areas and a committed wildlife protection staff. More recently, government wildlife conservation efforts and the ecotourism industry have been revitalised. Lake Mburo National Park in the south-west and the Kidepo Valley National Park in the north-east retain the largest and most viable plains zebra populations at present, although both continue to suffer from illegal hunting for meat and rapidly increasing livestock populations in the surrounding areas (E. Buhanga *in litt.* 7/97; Lamprey and Michelmores 1996).

Stable populations of Crawshaw's plains zebra currently occur in two countries: Malawi and Zambia (Figure 4.4). Northern Mozambique, despite suffering many years of

Figure 4.3. The locations and current sizes for known populations of Grant's zebra (*E. b. boehmi*) occurring on either governmental or private lands.



civil war and extirpation of its wildlife, has at least one remnant Crawshay's population.

Despite its small size, 11% of Malawi's total area consists of national parks and game reserves, demonstrating this country's strong commitment to wildlife conservation. Of these, two national parks and two game reserves support plains zebra populations, which are confined to these four areas by the surrounding agriculture and development (F. Mkanda *in litt.* 3/97; H. Nsanjama *in litt.* 4/97). Populations in Kasungu National Park and Vwaza Marsh Game Reserve have declined sharply since 1989, probably due to increased levels of poaching (Mkanda 1993). However, plains zebra are not a preferred source of meat in Malawi (Munthali and Banda 1992), so other factors may actually be responsible for these declines. Since plains zebra numbers elsewhere have increased or remained stable since 1989, the country's total population has not changed significantly over this period.

Zambia formerly had one of the best managed networks of protected areas in Africa. Unfortunately, during the last 15–20 years, wildlife protection efforts have diminished, resulting in increased levels of poaching and more frequent incursions of livestock into protected regions. External support has been vital to sustaining the Luangwa Valley national parks, which, together with their neighbouring game management areas, harbour over 90% of the total global population for the Crawshay's subspecies (Table 4.3). Within this complex of protected lands, plains zebra populations have either been stable or have increased slightly where good wildlife protection remains in force

(Jachmann and Kalyocha 1994). Less-protected populations, however, have continued to decline. An upsurge in game ranching over the past five years offers some potential for further increasing Crawshay's numbers in Zambia, as it does for the Upper Zambezi subspecies, provided ranchers consider the origins of their stock. Crawshay's is notable among the subspecies of plains zebra in that its lower incisors lack an infundibulum (Groves 1974). It may therefore be quite genetically distinct from the neighbouring Grant's, Upper Zambezi, and Chapman's subspecies and warrant special conservation focus.

The Niassa Game Reserve, along Mozambique's northern border with Tanzania, currently harbours a small population of Crawshay's zebra. However, zebra also occur still in the surrounding areas and recently proposed plans to expand the Reserve would augment its zebra population considerably (Leo-Smith *et al.* 1997). Encroachment by agriculture during the civil war and poaching remain the biggest threats to these animals. Tourism is also being regenerated though and may help to improve wildlife protection in the region.

Zambia is also the last remaining stronghold for the Upper Zambezi subspecies of the plains zebra (Table 4.3, Figure 4.5). The Kafue, Blue Lagoon, and Lochinvar National Parks, in addition to surrounding game management areas such as Kafue Flats, form a large protected area in west-central Zambia that supports approximately half the global population of the Upper Zambezi subspecies. Although currently stable, the Kafue

Figure 4.4. The locations and current sizes for known populations of Crawshay's zebra (*E. b. crawshayi*) occurring on either governmental or private lands.

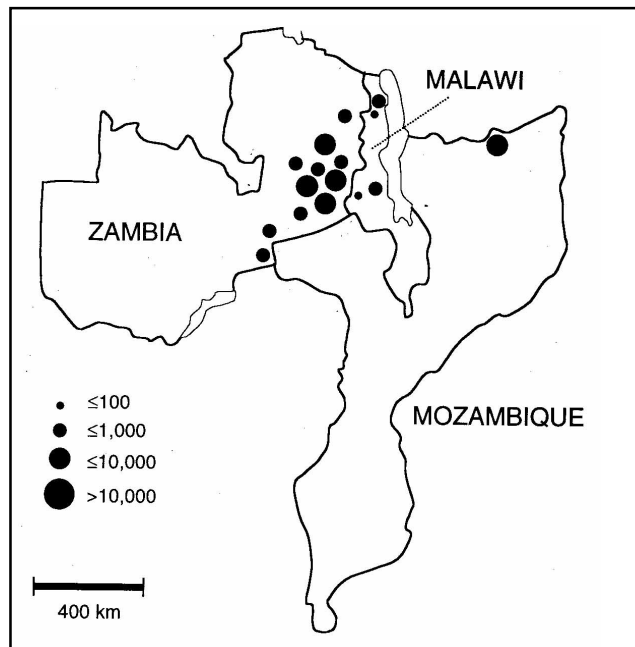
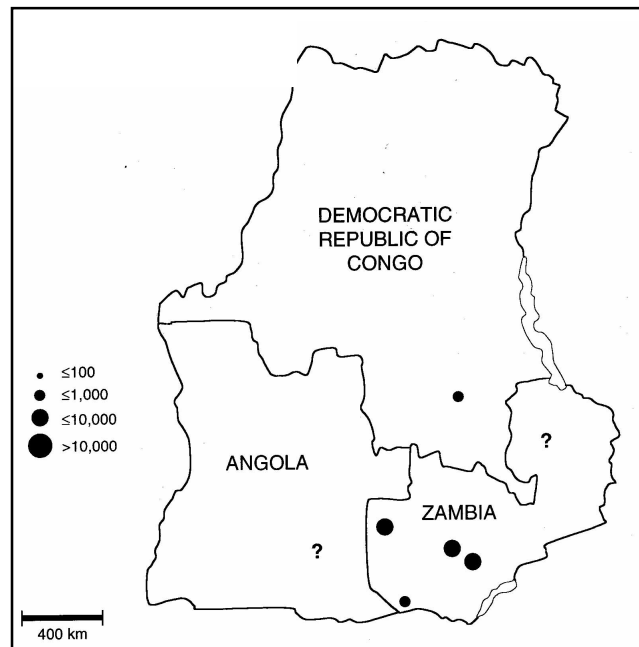


Figure 4.5. The locations and current sizes for known populations of the Upper Zambezi zebra (*E. b. zambeziensis*) occurring on either governmental or private lands.



population will likely increase if anti-poaching efforts improve as expected (Yoneda and Mwima 1995). An important population of Upper Zambezi plains zebra also occurs further west in the remote Liuwa Plain National Park where it is one of the most abundant ungulates. Many parts of Zambia, including game management areas in the Kafue region and the north-west, north-east, and east-central regions of the country, have not been surveyed within the last decade or more. Significant numbers of the Upper Zambezi subspecies may be currently unaccounted for in these areas since habitat generally remains intact and human and livestock densities are low.

The Upper Zambezi subspecies also occurs in eastern Angola and the southern Democratic Republic of Congo (formerly Zaire). Civil war in Angola during much of the past 25 years has devastated its wildlife populations, including its once-abundant plains zebra (see also Damara section), and destroyed the national parks administration and infrastructure (IUCN/ROSA 1992). Consequently, the Upper Zambezi plains zebra is probably extinct or nearly so in Angola, although confirmation will have to wait until future surveys are conducted.

Long-lasting civil strife and the chronic decay of governmental authority in Congo has also led to large losses of its wildlife. Upper Zambezi plains zebra formerly occurred in the southern grasslands and woodlands of the Upemba and Kundelungu National Parks, but had been extirpated from Kundelungu by the 1980s (Duncan 1992a). As of 1991, plains zebra still occurred in Upemba, but this population has almost certainly decreased since 1975, when the animals were estimated to number 1,000 (Verschuren 1975). Continued instability in the region may finally push this remnant population to extinction, if it has not done so already.

The Chapman's subspecies of plains zebra occurs primarily in Zimbabwe, but a small, declining population also resides in north-eastern Botswana (see the Damara section for a discussion of Botswana's plains zebra) and remnant populations may still exist in southern Mozambique (Figure 4.6, Table 4.3). As noted above for Crawshay's zebra, civil war has devastated Mozambique's wildlife populations and wildlife protection infrastructure. Fortunately, much habitat remains intact in formerly protected regions, such as Gorongosa National Park and the Marromeu Game Reserve. Externally funded efforts are currently in progress to protect remaining populations in these areas, and to rebuild the region's wildlife management and ecotourism infrastructures (Dutton 1994; Oglethorpe and Oglethorpe 1996).

In Zimbabwe, a long-established and well-developed system of protected lands maintains a stable or slightly increasing overall population of Chapman's zebra. National parks and safari areas cover over 12% of the country and support a growing ecotourism industry (Child 1995). Plains zebra concentrate in a string of protected

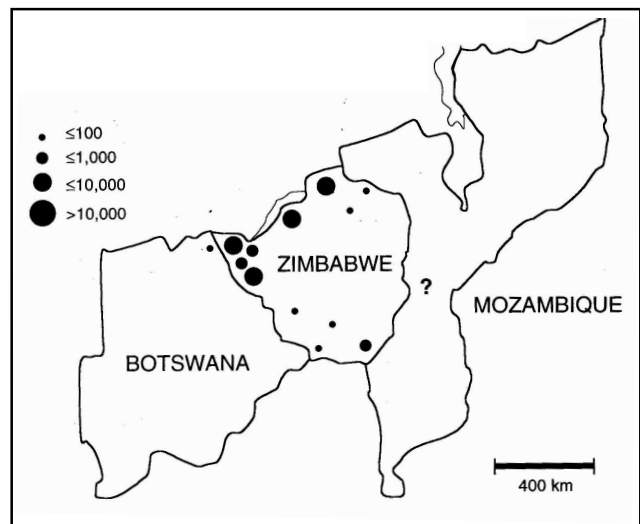


Figure 4.6. The locations and current sizes for known populations of Chapman's zebra (*E. b. chapmanni*) occurring on either governmental or private lands.

areas that begins on the border with Botswana in the west and arcs north along the Zambezi Valley, with nearly a third of the total population on protected lands occurring within the Hwange National Park and the adjacent Deka Safari Area. In recent years, chronic funding shortages have eroded the general infrastructure for wildlife protection and management but, so far, poaching remains at generally low levels (Dublin *et al.* 1994; Meldrum 1996).

In addition to Zimbabwe's parks and safari areas network, private game ranches and communally managed lands support a large number of plains zebra. Indeed, slightly more than half the country's total population resides on these private lands, which together constitute 37% more area devoted to wildlife than protected, government lands (Kock 1996). The transfer of wildlife ownership from the government to landowners has generally benefited conservation by providing economic incentives to manage wildlife as a valuable resource rather than extirpate it as a direct competitor with livestock and agriculture (Child 1995). Levels of protection and management are higher on many game ranches than they are on protected lands and reduced stocking levels of cattle have allowed ranges to recover from overgrazing. Whether this positive trend continues depends critically on the profitability of ecotourism, trophy and sport hunting, and the live animal trade since meat production alone is insufficient to support game ranching (Style 1991). On communal lands in particular, trophy and sport hunting generate 90% of the revenue gained from wildlife (Kock 1996). The sustainability of game ranching also depends on governmental attitudes towards it, which have the potential to shift quickly with domestic political and economic changes or in response to international pressures.

From a taxonomic perspective, Chapman's zebra may be near extinction, or have never existed. The interpretation presented by Duncan (1992a) implies that pure Chapman's zebra only live in southern Mozambique, while those in Zimbabwe and Botswana represent hybrids with either Crawshaw's or Damara zebra. Evidence from stripe patterns suggests that intergradation with Damara zebra does occur in western Zimbabwe (Skinner and Smithers 1990). Some taxonomists recognise an alternative subspecies, *E. b. selousii*, as occupying the eastern half of Zimbabwe and extending to variable degrees into Mozambique (Roberts 1951; Sidney 1965; Kingdon 1979). This is a conflict that is only likely to be resolved through extensive genetic sampling of plains zebra in Zimbabwe and its immediate neighbours. The current expansion of game ranching and trade in live animals in this region will likely add to this taxonomic confusion.

The Damara subspecies historically ranged across southern Africa, from Swaziland, Lesotho and South Africa in the east through northern Botswana to Namibia and Angola in the west (Figure 4.7). As reported above for the Upper Zambezi subspecies, Angola's population of Damara zebra is probably gone, although future surveys may disprove this conclusion. Similarly, no Damara zebra remain in Lesotho at this time (Castley *in litt.* 8/97). Extant populations of this subspecies occur primarily in Botswana and South Africa, but Namibia also supports a significant percentage of this subspecies' total population (Table 4.3).

Namibia retains extensive areas of relatively unmodified natural habitat, has a well-developed system of protected areas, and supports a strong wildlife utilisation industry. A single, large, protected population of plains zebra is confined by fencing to Etosha National Park, while smaller numbers are scattered elsewhere in the north on private ranches and communal lands. Etosha's population declined by more than 75% from 1960 to 1985 due to hunting and the fencing of their range, but numbers have been stable or only slowly declining since then (Gasaway *et al.* 1996). In contrast, between 1972 and 1992 the number of plains zebra on commercial farmlands has increased more than three-fold. The economics of wildlife utilisation in Namibia currently favour the joint ranching of both cattle and game, but as more landowners join together in conservancies to manage their lands as a single unit, economies of scale will favour a greater bias towards wildlife production (Barnes and de Jager 1996). Larger blocks of land also increase the potential for ecotourism, the most profitable form of wildlife utilisation at present.

Botswana retains several large populations of Damara zebra in the north of the country, centred around a few protected areas. This protected region, although extensive in area and now the basis for a substantial ecotourism industry, was established with greater regard for the

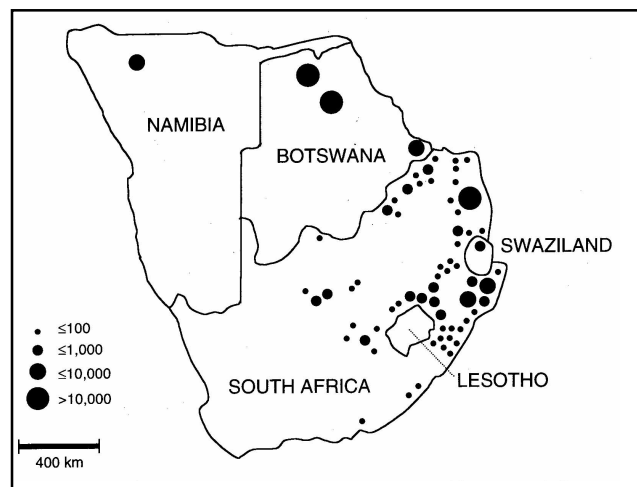


Figure 4.7. The locations and current sizes for known populations of the Damara zebra (*E. b. antiquorum*) occurring on either governmental or private lands.

The numerous game ranch populations on private lands in the Tuli Block, south-eastern Botswana, have been aggregated and considered as a single unit. The locations and sizes of populations on private and communal lands in Namibia are currently unknown, although they are concentrated in the northern half of the country and an overall total figure for these populations is included in Appendix 3. All nationally protected and most provincially protected lands in South Africa have been indicated, but populations on private farms are too small and numerous to plot (see Appendix 3 for estimated totals occurring on these private lands).

avoidance of major areas of human settlement and cattle ranching than for the ecological requirements of wildlife (Campbell 1973). Given current funding and staff shortages in the government's wildlife management infrastructure, a lack of progressive management and conservation policies, and further expansion of human activities (Crowe 1995), Botswana's zebra numbers are expected to decline. Nevertheless, Botswana's government is currently making serious attempts to improve wildlife protection and management. If these attempts are successful, the country's protected areas should be able to support significant zebra populations for the foreseeable future.

The largest remaining Damara population in Botswana, occurring in the Okavango-Chobe region, is currently threatened by a Namibian scheme to divert water from the Okavango River, and thus the vital dry season range of the Okavango Delta (Hannah *et al.* 1997). Both this population and the neighbouring population of the Makgadikgadi Pans and Nxai Pan National Parks are totally reliant on unprotected areas for part of their seasonal migratory cycle. Human encroachment (Kgathi and Kalikawe 1993) and further fencing of the range to impede the spread of cattle diseases (Hannah *et al.* 1997) pose immediate threats to these crucial areas. The only other plains zebra in Botswana occur on the north-eastern border with Zimbabwe, where numbers have declined by more than

40% per annum since 1990 (Department of Wildlife and National Parks 1995), and in the far eastern Tuli Block, where numbers are increasing on private farms. Those on the Zimbabwe border move seasonally between the two countries and are apparently of the Chapman's subspecies (see above).

By the early part of this century, overhunting and human encroachment had extirpated two of South Africa's plains zebras – Burchell's and the quagga – and restricted the remaining Damara zebra to a narrow strip along the north-eastern edge of the country (Kruger National Park and northern KwaZulu-Natal Province: Castley and Knight 1997). However, great efforts have been made during the last several decades to preserve remaining populations and reintroduce Damara zebra to areas of their historical range. Numbers of this subspecies are stable or increasing in at least four small national parks throughout the northern half of the country. The huge Kruger National Park supports an increasing population that represents over 60% of the country's total, making it critical to the long-term welfare of this species in South Africa. The Kruger also serves as the main source of stock for founding new populations in other national parks or supplementing existing ones. Unlike the plains zebra in most other protected areas throughout Africa, those of South Africa are confined by fences, making them more vulnerable to droughts in some cases (Walker *et al.* 1987) and requiring very active population management. Poaching is less of a problem than in other countries due to better protection and an apparent dislike for the meat in most of South Africa's indigenous cultures, although snares intended for other wildlife often kill zebras instead.

More recently, Damara zebra numbers in South Africa have been augmented by a rapid growth in the size and number of populations on provincial game reserves, private game reserves, and game ranches. In many cases, stock for founding populations on private reserves and ranches have come from other private lands, creating a significant market in live animals (M. Knight pers. comm., 1997). Genetic considerations are not generally taken into account when translocating zebra – nor are quarantine measures in force in most cases – although provincial reserve managers may use multiple translocations from different areas to increase the genetic diversity of founder populations (A. Armstrong *in litt.* 9/97). Most farm and reserve populations contain fewer than 100 individuals, and many have less than 50, increasing the likelihood of further reductions in genetic diversity due to inbreeding. Active management for trophy hunting and venison production will also likely alter the age structure and adult sex ratio from what they would be in natural populations. Thus, Damara zebra are reclaiming much of their historical range in South Africa but with an unnatural population structure in most cases and possibly an altered social organisation as well. The

specific long-term effects of these changes on population viability and productivity are unknown at present, but they could be quite detrimental (Ginsberg and Milner-Gulland 1994). Research directed at these issues is urgently needed given the widespread trend in other countries towards South Africa's current situation of many small, confined plains zebra populations, managed for a range of extractive and non-extractive uses.

4.10 Captive populations

The plains zebra is widely held in zoological collections throughout the world. According to the International Species Information System (ISIS), the total global population for this species in captivity numbers approximately 1,060 individuals. Of these, over 75% derive from only two of the six subspecies: 41% are Grant's subspecies and 36% are Damara subspecies. No zoological park members of ISIS appear to hold populations of either Crawshay's or the Upper Zambezi subspecies. The ISIS database encompasses 500 zoological institutions located in 54 countries, yet this represents only half those found worldwide. The total captive population of plains zebra is thus likely to exceed 2,000 individuals, and unrepresented subspecies may actually occur in some non-ISIS collections, although they are likely to be few in number. Plains zebra apparently breed easily in captivity given that 18–24% of captive adult females in the ISIS database currently have foals.

4.11 Threats and conservation issues

The principal threats to plains zebra are similar to those faced by other large ungulates throughout Africa: loss of habitat and overhunting. Although no country within this species' range is free of either problem, loss of habitat appears to be more of a concern in the southern half of the plains zebra's range, while poaching appears to be more significant in the northern half. This difference between regions may simply reflect a more advanced state of development in the south, where fewer large tracts of unmanaged range remain.

Expanding human populations have caused settlements and crop agriculture to also expand, reducing the area of suitable habitat available and cutting off migratory corridors. This effect is most extreme in countries with long histories of development (South Africa) and smaller countries with high human population densities (Malawi, Rwanda). In such cases, free-ranging plains zebra populations have ceased to exist, introducing a new set of threats inherent to small confined populations (see below). In range areas unsuitable for crops, competition with livestock for water and grass has led to the hunting and

fencing of plains zebra off the range. But the profitability of modern livestock ranching usually requires higher stocking densities than a range can sustain, reducing its productivity and even further exacerbating competition with wild grazers such as plains zebra. In pastoralist communities (e.g. Masai of Kenya and Tanzania), plains zebra have traditionally coexisted with the livestock, but recent trends towards the development of crop agriculture and permanent settlements on these lands do not bode well for the future of this coexistence.

Illegal hunting of plains zebra for meat has severely depleted populations throughout the species' range. Legal hunting may also be responsible for plains zebra declines in some areas since rates of sustainable, but indiscriminate, harvesting, in the range of 10–15% per annum, are almost certainly unsustainable in most habitats (see above). The magnitude of the poaching threat is closely tied to the level of wildlife protection a country is able to support; a few fenced areas (Namibia, South Africa) are clearly easier to police than huge tracts of open range (Kenya, Tanzania). Insufficient resources hamper wildlife protection in many countries, often forcing authorities to focus on key areas while leaving other nominally protected areas unsupervised (Zambia). International support, in the form of training, salaries, and equipment, could have a large impact for the better on this problem. Fortunately, plains zebra are killed primarily as a source of food and the meat is mostly consumed in nearby communities, making it a locally, rather than an internationally driven phenomenon. Relatively simple solutions to this problem may then be possible. For example, revenue-sharing programs between tourist areas and the surrounding communities in order to derive an alternative value from wildlife, or community ownership of wildlife to encourage its conservation and husbandry as a valuable, utilisable resource (e.g. CAMPFIRE in Zimbabwe).

Both threats of poaching and habitat loss become greatly magnified when civil strife erodes the power of wildlife protection authorities, displaces people and their livestock from their usual homes, destroys the normal food production and distribution mechanisms creating a greater demand for game meat, and provides the weaponry to acquire this game. Indeed, given the rapidity with which plains zebra numbers have fallen to extinction levels in countries such as Angola, Mozambique, and the Democratic Republic of Congo (Figure 2) – all of which have suffered through recent civil wars – political instability may be the most critical, over-arching threat to the long-term welfare of plains zebra in the wild. Even short episodes of instability can be damaging if they scare away vital tourist revenue in countries where the wildlife protection infrastructure depends heavily on this source of support. This is likely to become an even greater problem in the future as regional and global competition within the ecotourism market increases.

A less tangible, but perhaps very important future threat to the long-term welfare of the plains zebra in the wild is, ironically, the rapidly growing industry of game ranching. If done properly, game ranching could be a very important tool for conserving plains zebra whilst also improving human welfare in a sustainable manner. However, wide-scale translocations of animals without concern for the possible genetic or disease-related consequences of these movements could, conversely, have a negative impact on remaining natural populations. The plains zebra occupies a huge range in Africa and is adapted to a large variety of habitats. Specialised adaptations to local conditions could conceivably be degraded by a human-supported influx of animals from an ecologically different part of the species' range. Similar translocations could introduce new pathogens and parasites to populations without co-evolved resistance to them. Caution must be exercised in the stock chosen for translocations and the spatial scale of these movements until we learn more about the genetics and diseases of the plains zebra.

Overall, the plains zebra is a relatively resilient species that has demonstrated a remarkable ability to recover from population declines when provided with suitable habitat and protection from overhunting. Indeed, population growth rates as high as 23% per year have been observed within a few years of reintroduction to at least one national park in South Africa (Castley and Knight 1997). In the current climate favouring the sustainable use of wildlife as the ultimate, long-term source of protection, the plains zebra should fare very well since not only is it a good source for meat, skins, and other trophies, but its natural beauty and global recognition make it an essential component of the fauna sought by ecotourists.

4.12 Proposed actions

4.12.1 Improve coverage and pace of global monitoring

The data presented within this Action Plan represent the most thorough and accurate account of the population sizes, locations, and conservation status of plains zebras globally. However, although it is more comprehensive than all similar attempts to date, there is still much room for improvement. Significant regions remain unsampled in the last ten years, even in countries with well-developed wildlife protection infrastructures. The rapid pace of change in many African nations requires annual or biennial sampling if we are to detect environmental problems in their early stages and more effectively respond to them. In this regard, international support can play a major role by establishing and maintaining vital ecological monitoring programs until host nations are able to assume these responsibilities themselves.

4.12.2 Improve risk assessment

A global perspective on the status of the plains zebra is a necessary component of any plan to conserve this species, but most of the important conservation battles will be fought population-by-population, site-by-site. This requires a more detailed and forward-looking database of development patterns in order to highlight where future conflicts with wildlife will occur, and to guide efforts for mitigating the likely human impacts. For example, many plains zebra populations centre around protected areas but, for at least part of their annual cycle, depend critically on food and water sources in unprotected regions. Future development in the latter regions will consequently have profound effects on the long-term viability of these nominally 'protected' populations.

4.12.3 Quantify and manage genetic diversity, globally and locally

On the global level we must resolve whether current subspecific designations refer to genetically distinct entities, and therefore require separate management plans. This information is becoming more critical as game ranching and efforts to reintroduce the species to former parts of its range increase the frequency and scale of artificial translocations. We also need to identify genetically critical populations or those whose loss would substantially diminish the species' global genetic diversity. More locally, we need to monitor the genetic consequences of reduced population sizes in two principal contexts: (i) as human development restricts populations, causing them to shrink into protected areas and (ii) as game ranching leads to the proliferation of small, intensively managed populations. Determining the impacts of culling and cropping programs in both these contexts is also integral to monitoring genetic diversity at the local scale.

4.12.4 Increase understanding of species' basic biology

Too little is currently known about population regulation in natural plains zebra populations to predict how they will respond to increasing human-induced changes in their environment (e.g. elimination of predators, partitioning of the range, proliferation of cattle and other livestock). Neither do we know enough about the species' basic demography to determine sustainable harvesting rates in natural populations, nor to predict the impacts of specific harvesting programs on recruitment in confined, actively managed populations. Included in these impacts are disruptions of the plains zebra's unusual social organisation, which may then indirectly lower recruitment levels. We also need to determine the extent of natal dispersal for each sex and, in specific cases, the scale and timing of seasonal migration patterns if we are to understand the processes regulating genetic diversity within and between natural populations. Finally, plains

zebras are clearly important members of the grassland communities in which they live, but their specific roles in shaping the structure and dynamics of these communities are as yet unknown.

4.12.5 Investigate the economics of alternative utilisation strategies

In acknowledgement of the changing worldwide climate in conservation towards making wildlife pay its way (Eltringham 1994), we need to study the several utilisation options available for plains zebra. This species represents an excellent source of meat and produces beautiful skins, but it is also a globally recognised symbol for Africa's savanna wildlife and therefore a powerful attractant for both ecotourism and international support for wildlife protection. The comparative economics of these alternatives must be considered, taking into account the differing circumstances within particular countries and regions, if we are to guide the global management of this valuable species. Quantifying how plains zebra are currently being utilised in each country and determining the proportional economic contributions of these uses is an urgently needed first step in this direction.

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