Status, distribution and structure of Grevy's zebra populations in northern Kenya

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Abstract

This thesis presents the results from a survey carried out across the entire range of Grevy's zebra in northern Kenya. The aim of the survey was to quantify accurately the overall population size and distribution using mark-recapture techniques, and to investigate the effects of livestock on the comparative structure and ecology of different Grevy's zebra populations.

The final estimate of 2571 (95% confidence interval 2435 – 2707) Grevy's zebra in northern Kenya is reliable with narrow confidence limits. This represents a 40% decline since the (less robust) 1992 estimate. Estimates and distribution data for individual populations show fragmentation and possible isolation in the north of their Kenyan range. Nearly 3000 hours of work has produced a key output: 74% of all Grevy's zebra in northern Kenya are identified in a digital database. The current distribution of all populations and water sources are also mapped.

In arid areas, high livestock density had a negative effect on recruitment within Grevy's zebra populations. In these populations there were fewer lactating females with foals aged 0-6 months – and those that there were, were found significantly further from water. In areas with high livestock densities Grevy's zebra populations ranged over smaller areas and were found in over-dispersed and larger aggregations. These populations are threatened not only by the processes driving their current decline, but also by processes inherent within their small size and isolation.

These results must be understood within the framework of the intrinsic heterogeneity in resource distribution that exists in human exploited semi-arid ecosystems. It is the maintenance of this heterogeneity that will allow these small and potentially isolated populations, and ultimately the species as a whole, to persist.

Acknowledgements

Faced with a blank page and swirling memories – nostalgia takes over, and even the low points are gilded into happy reminiscence. That transformation, and of course the culmination of the work, are wholly attributable to the people mentioned below. But that tribute, coupled with profound thanks still seems woefully inadequate. It is – but nonetheless, to all who contributed, below and inadvertently forgotten, my deepest gratitude, and memories forever.

For perspective, this work required nearly 3000 hours of scanning, assessing and matching photographic images. There were many times when this task seemed beyond me – it would have been without the motivation, belief, and support in all forms from so many. Oh my god…it's over!

The work was initiated by Stuart Williams, whose support since – supervisory, culinary and motivational – has been vital. His generosity, and willingness to resort to bribery and extortion to see me get this to completion have been crucial. But above all, Stuart, Sophie, Gabriel and Leo have welcomed me into their family and home in Ethiopia, fed me, laughed with me, and played dinosaurs with me. That's why it's over. I'm coming back.

The Government of Kenya allowed the survey to be conducted, clearance was received from the Provincial Administration of the Office of the President (Permit Reference Number: MOES & T/13/001/23C 2/23). The survey was conducted in affiliation with the Kenya Wildlife Service (KWS). Three KWS field staff worked with the survey in the field - Bernard Koloba, Samuel Ambassa and Francis Omondi. Local politics and bureaucracy were never a match for Bernard's patience and eternal good-humour.

Martin Mulama provided support for the survey in the KWS HQ in Nairobi. In addition, the rangers from KWS Special Operations provided security for the survey while in the Isiolo-LMD area and information on the security situation in other areas. They were a delight to work with – professional, motivated and tough, yet warm, friendly and hospitable to 'their' area.

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Study buddy...Graham Hemson beat me to submission by three days, cut and ran. Thanks for the infectious humour Graham. Andy Loveridge read and commented on parts of the thesis with superhuman rapidity. Stephen Gregory volunteered to help with some of the image analyses, and even worked with me until late into the night! Thank you Steve...you deserved a holiday in the Galapagos! For good humour, warm cheer, and wonderful memories (HH and more recently Linacre Bar) I am indebted to all in the WildCRU...Mike H, Deb, Paul, Em, Graham, Greg, Lise, Lucy, Mike T, Stephen, Donna, Roo, Andy L, Sandra, Hannah, Andy S, Tom...to name but a few.

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1. General introduction

Conservation efforts are driven by an attempt to reduce biodiversity loss (Balmford *et al.*, 1998; McShane, 2003), where diversity is measured over different hierarchical scales of biological organisation, from genes to populations, species, communities and beyond (O' Neill, 1989). Generally, efforts are focused at the population, species or community level and employ measures of population or species abundance, and species richness, in assessing diversity (Brooks *et al.*, 2001; Pimm *et al.*, 1995) – even for more recent ecosystem approaches (Balmford *et al.*, 2003). The conservation threats to species are typically recognised and measured by reductions in range and/or population size (Butchart, 2003; IUCN, 2003; Lamoreux *et al.*, 2003).

Caughley (1994) highlighted a fundamental conceptual dichotomy within conservation biology. He argued that conservation biology's dual origins have given rise to two fronts: the declining-population paradigm, concerned with factors extrinsic to the population at risk (e.g. competition, habitat loss); and the small-population paradigm, concerned with factors intrinsic to the population (e.g. demographic and genetic stochasticity). He recommends a 'cautious mixing' of both approaches to tackle conservation problems.

Asquith (2001) believes that reconciling the two paradigms is more difficult than it appears. He argues that conservation biologists make assumptions too easily, often based on background and experience, and that simply identifying the problem and then choosing the correct methodology is the most effective starting point. Problem identification typically starts within the declining-population paradigm, i.e. quantifying rate of decline and trying to understand the mechanisms driving the decline (Caughley & Gunn, 1996). But this is not to say that it should end there, the innate characteristics of small populations can render them vulnerable to extinction by stochastic processes or disturbances that are sometimes unrelated to the mechanisms that have driven the decline.

Abundance estimates, or an understanding of population size are fundamental for both paradigms; and knowledge of the ecological and social forces shaping population demographics are necessary to understand the threats to persistence and the risk of extinction, and to design effective conservation strategies. Changes in abundance over time or space allow us to quantify rates of change and hence draw assumptions about the underlying mechanisms driving this change, to test hypotheses regarding these mechanisms, and to test the effectiveness of intervention strategies.

This study was initiated as a first step in identifying and tackling the problems that have lead to the largely anecdotal population and range declines (Grunblatt *et al.*, 1996; Rowen & Ginsberg, 1992; Wisbey, 1995) of Grevy’s zebra (*Equus grevyi* Oustalet). It aims to: 1) quantify accurately population sizes using individual identification and mark-recapture techniques, and 2) investigate comparative structure and ecology of different Grevy’s zebra populations as a key to understanding their conservation requirements.

1.1 Abundance estimation

Abundance estimates are typically drawn from samples rather than total population counts. Estimates are made from count statistics (e.g. number of animals caught, seen or heard) which are related to the actual population size by a sampling fraction – reflecting the spatial sampling and the observability of the sampled population (Conroy & Nichols, 1996; Thompson *et al.*, 1998; Williams *et al.*, 2002). Using this framework, Lancia *et al.* (1996) described the following general estimator for the number of animals in a population $\hat{N} = C/(\hat{a} . \hat{p})$, where $\hat{N}$ = estimated number of animals in the population within the total area, C = count statistic (number of animals counted during the survey), $\hat{a}$ = estimated proportion of the total area surveyed, and $\hat{p}$ = estimated proportion of animals occurring in the surveyed area that were counted.

There are numerous sampling methods which allow a and p to be modelled and then combined with the count statistic C to derive estimates of population size; e.g. capture-mark-recapture, removal and resight methods, quadrant counts, and line-transect and distance methods (Krebs, 1999; McCallum, 2000; Southwood & Henderson, 2000; Thompson *et al.*, 1998; Williams *et al.*, 2002). Ecological, economic and statistical factors must all be considered when choosing an appropriate sampling method. Rare species might be at too low a density to obtain valid estimates within a reasonable sized plot, while high density populations might make some techniques too time-consuming.

If the whole area can be surveyed (preferably repeatedly) and individual animals are easily recognised, then capture-mark-recapture methods provide a good means of estimating the probability of observation (p). They compare information derived from the initial captures/sightings with subsequent recaptures/resightings – hence $\hat{N} = (CM)/R$, where C = total number of individuals captured in sample t+n, M = number of individuals marked at sample t, and R = number of individuals caught in sample t+n that are marked (Krebs, 1999; Sutherland, 1996).

1.1.1 Capture-mark-recapture techniques (CMR)

The typical CMR study provides two distinct types of information: the recapture of marked individuals and proportions of marked:unmarked individuals captured at each sampling time (Nichols, 1992). Data from the former are used to estimate 'survival' (death/emigration) rate, whereas both types of information are necessary to estimate abundance or the number of ‘births’ (births/immigration) (Young & Young, 1998). CMR models vary according to whether the population is closed or open.

1.1.1.1 Closed populations

Closed populations are those where it can be assumed that there have been no births, deaths or migration (e.g. in short-term studies of five to ten days for large animals) and thus only abundance is being estimated (Otis *et al.*, 1978; White *et al.*, 1982). The capture histories of individual animals over time are modelled in terms of capture probabilities. The simplest model (or null model – M_o) assumes no variation in capture probabilities and is rarely biologically correct. This model serves better as a baseline against which to judge departures from the ideal (Otis *et al.*, 1978). Three principal sources of variation are recognised: 1) heterogeneity, M_h, which accounts for the inherent variability in capture probability amongst individuals, 2) behavioural response, M_b, accounting for changes in an individual’s behaviour as a response to capture, e.g. trap avoidance or trap ‘happy’ responses, and 3) time, M_t, accounting for temporal variation or conditions that might affect capture probabilities, e.g. different weather conditions.

1.1.1.2 Open populations

Open population models allow for additions to (birth and immigration) and deletion (death and emigration) from the population (Lebreton *et al.*, 1992; Pollock *et al.*, 1990). Capture histories resulting from studies of open populations are modelled using capture probabilities and survival probabilities. These models estimate population size, survival rates (mortality/emigration), birth rates (reproduction/immigration) and probability of capture for each sampling period. They are thus appropriate for long-term studies of large mammals, but because of the numerous parameters large amounts of data must be collected in order to estimate these parameters with reasonable precision (Lebreton *et al.*, 1992).

1.1.2 CMR for large mammals

CMR techniques have been considered less suitable for studies on large mammals as precise estimates of abundance require relatively large sample sizes, frequent trappings and high probabilities of capture (Rosenberg *et al.*, 1995; White *et al.*, 1982). However, more recently the use of natural markings in conjunction with extensive photographic data has helped to reduce effort involved in 'capture' and overcome biases in population estimates by increasing the number of marked animals in the population and their capture probabilities; e.g. humpback whales (Smith *et al.*, 1999), Mediterranean monk seals (Forcada & Aguilar, 2000), bottlenose dolphins (Gowans & Whitehead, 2001; Wilson *et al.*, 1999), tigers (Karanth & Nichols, 1998), white-tailed deer (Jacobson *et al.*, 1997; Koerth *et al.*, 1997), and black rhinos (Emslie & Brooks, 1999)).

Using individual markings as natural tags has advantages: the animals do not have to be physically handled, there are no tags to possibly affect behaviour, and they are often large, readily visible and permanent. There are possible disadvantages: the markings could change with time, there is a chance of animals sharing indistinguishable markings, and the process of recognition and matching takes longer and has the potential for more errors (Forcada & Aguilar, 2000; Hammond, 1990). The inclusion of poor quality or indistinguishable images has been found to bias abundance estimates (Forcada & Aguilar, 2000; Gowans & Whitehead, 2001; Stevick *et al.*, 2001).

More recently methods have been developed to take advantage of the growing amount of radio-telemetry work (Arnason *et al.*, 1991; White, 1996a; White & Shenk, 2001). Radio-tagged animals are considered the marked animals (although any marking method that allows animals to be sighted at a distance can be used), and estimates are based on the frequencies of resightings of marked animals within the population as a whole over subsequent survey periods (Krebs, 1999).

1.2 General biology and conservation status of Grevy's zebra

As a background to this study I will briefly describe the distribution, numbers, threats and basic ecology of Grevy's zebra, and then discuss the implications of these for a survey that aims to estimate population numbers.

1.2.1 Status, distribution and numbers

Grevy's zebra have undergone one of the most dramatic reductions in range of any African mammal and are now found only in northern Kenya and southern Ethiopia. Coupled with apparent considerable population declines they are now classified as Endangered by the IUCN (IUCN, 2003; Williams, 2002). They are also on CITES Appendix I (since 1979), banning any international commercial trade in Grevy's zebra or their products, including skins.

Grevy's zebra were thought to range historically from the Danakil desert in Eritrea and Djibouti, through the Awash valley in central Ethiopia, northeast of Lake Turkana, across northern Kenya east of the Rift valley, and into western Somalia (Fig. 1.1, Kingdon, 1997; Yalden *et al.*, 1996). They are now considered extirpated in Djibouti, Eritrea and Somalia (Rowen & Ginsberg, 1992; Williams, 2002), and are restricted to three known and isolated areas in Ethiopia. A recent intensive aerial and ground survey has preliminarily estimated a total population of 110 animals in Ethiopia (Williams *et al.*, 2003), an 80% decline since Thouless's 1995 (1995a; 1995b) estimate of 500-600 (based on low coverage aerial sample counts with high error limits, e.g. in one area an estimate of 30 was based on a sighting of only one zebra).

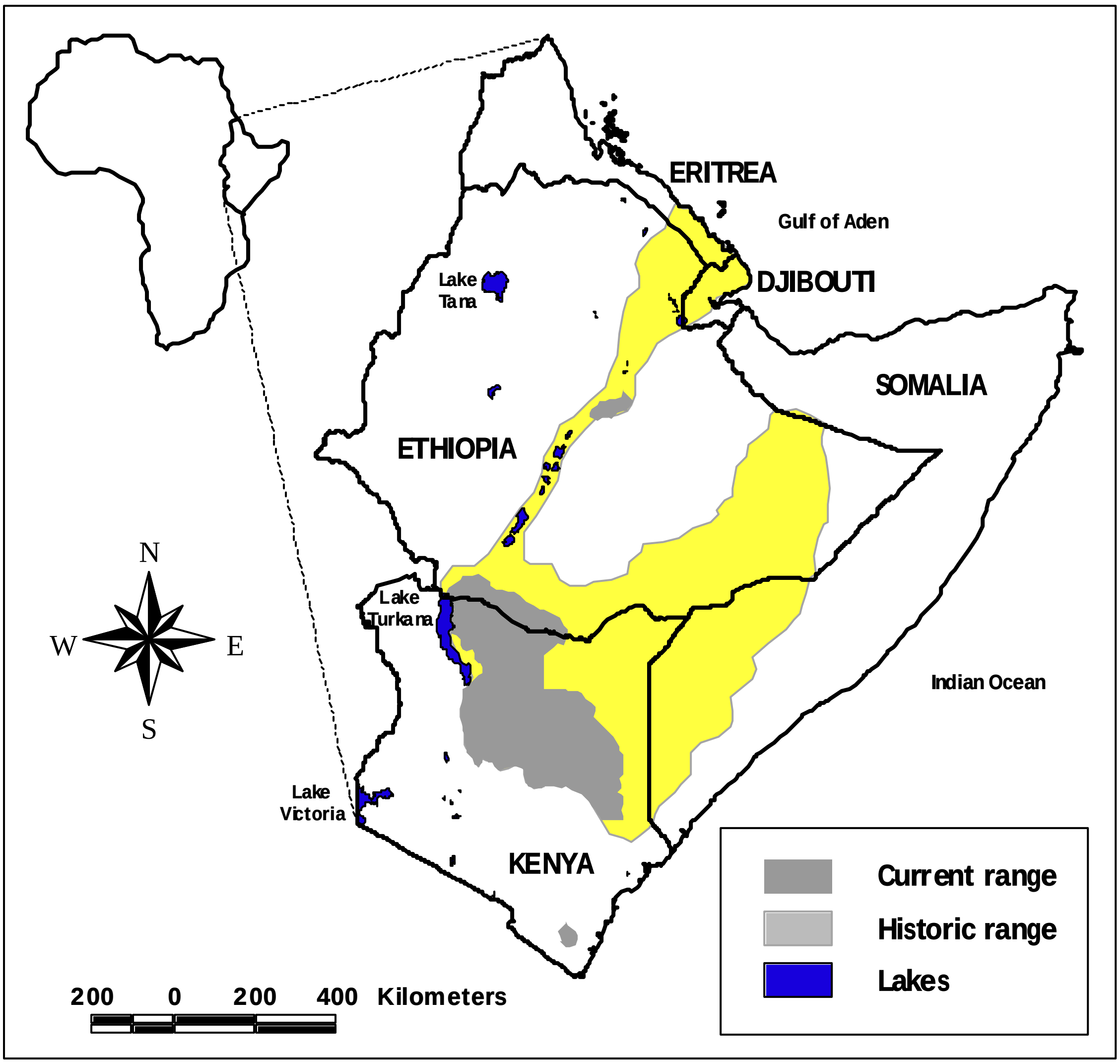

Figure 1.1: The historic and current ranges of Grevy's zebra in northern Kenya (from Kingdon, 1997; Williams, 2002; Yalden *et al.*, 1996).

Grevy's zebra are also much reduced in range and number in northern Kenya. In 1980, Klingel (1980) reported observing up to a 90% decline in some areas since the 1960's – although some of this decline could have been displacement caused by transformation of the rangeland through sustained overgrazing by livestock. Rowen & Ginsberg (1992) describe a 70% reduction from 1977 to 1988 (from 13700 to 4300 animals), using data based on sample surveys done by the Kenyan Department of Resource Surveys and Remote Sensing (DRSRS) and guesses for unsampled populations. More recently, a short survey throughout northern Kenya, that was unable to provide reliable population estimates, suggested that the northern populations, where they are almost exclusively forced to live sympatrically with pastoralists and their livestock, have become small and fragmented (Wisbey, 1995).

The DRSRS data follows the conventional method used to estimate wildlife numbers in Kenyan rangelands. Sample counts are conducted on a political district basis, with coverage ranging from 2-10% - typically about 5%. For a widely dispersed and low density animal such as Grevy's zebra – which are aggregated into groups, while home ranges of individuals of both sexes may be up to 10000 km^2 (Ginsberg, 1988) – the estimates are consistently unreliable, with extremely high standard errors (Grunblatt *et al.*, 1996; Muchoki, 2000; Williams, 2002). Further, the DRSRS counts were temporally sporadic (because of funding difficulties), making range-wide estimates impossible. The nature of sample aerial counting also makes it impossible to accurately assess local distributions, or possible connectivity between populations.

The only reliable quantitative data that exists for Grevy's zebra is for Lewa Wildlife Conservancy (a partially fenced reserve) – where total aerial counts have been conducted annually (six years are missing) since 1977 (2000 estimate was 497, Williams, 2002). Less reliable estimates from long-term ecological and social studies (Ginsberg, 1989; Rowen, 1992; Williams, 1998b) also exist for the population that is found in and around the Buffalo Springs, Samburu and Shaba national reserves (roughly estimated to be 1000 in 1998 – S.D. Williams *pers. comm.*). These reserves are an important source of permanent water, and act as key birthing and breeding areas.

The only area where Grevy's zebra numbers and range appear to have expanded is southward onto the Laikipia plateau, historically a marginal area for them. It is speculated that this range expansion is a result of movement away from lowland areas dominated by pastoralists and their livestock, with a concurrent reduction in domestic livestock density, an increase in artificial water sources and favourable habitat change on the Laikipia plateau. This could now be another crucial birthing area for Grevy's zebra (Williams, 2002).

1.2.2 Ecology and behaviour

Grevy's zebra are found in semi-arid to arid (annual rainfall range 100-650mm) grass/shrubland where permanent water is available. They are predominantly grazers with a caecal digestive system requiring a high food throughput, favouring quantity over quality. This forces them to feed in areas of highest vegetation biomass when food becomes limiting (Ginsberg, 1989; Rubenstein & Hack, in press; Williams, 1998b). Most importantly they require free-standing water as part of their diet – but most adults can tolerate up to five days without water while lactating females require water every one to two days (Becker & Ginsberg, 1990; Ginsberg, 1989; Rowen, 1992). The lack of permanent water ultimately limits their incursion into more arid areas to the east and north of their range, while competition with other grazers, including Plains zebras, is likely to limit their distribution into more mesic areas (Bauer *et al.*, 1994, D. Rubenstein, *pers. comm.* – work in progress).

Breeding males defend large resource territories (water and food being the key resources) where their mating success is dependent on the females attracted to the resources on their territory (Ginsberg, 1989; Klingel, 1974; Rubenstein, 1994). In contrast, a female's reproductive condition determines the priority she places on different resources. Thus, when the distribution of grazing allows it, lactating females are found close to water and mate with one male whose territory has access to water (Ginsberg, 1989; Rowen, 1992; Rubenstein, 1994; Williams, 1998b). However, in large parts of their range, where forage is sparse or the first 6-7 km from water has been altered by overgrazing by domestic livestock, lactating females must move large distances (up to 13 km – this study) to and from water to reach adequate grazing (Williams, 1998b). This means that they may move through a number of territories and mate with many males.

Non-lactating females are promiscuous, mating with males whose territories contain resources that have attracted them. Similarly, females without foals display fluid associations - their movements determined by the availability and abundance of resources (Ginsberg, 1989; Rubenstein, 1986). Females with young foals have far more predictable patterns of association, forming relatively stable and sedentary groups with other females with whom they are in reproductive synchrony (Becker & Ginsberg, 1990; Ginsberg, 1989; Rubenstein, 1986).

Williams (1998b) found that Grevy's zebra compete for critical resources with pastoralists and livestock. The seasonal limitation of forage in pastoralist areas, and predators were found to be important factors determining use of space. In the absence of pastoralists Grevy's zebra drink diurnally to avoid predation. In pastoralist areas the monopolisation of water sources by people and livestock forces them to drink nocturnally, and to move long distances between the areas with sufficient grazing and water. Foals do not travel to water with their mothers, but remain in "kindergartens" up to 8km from water (Becker & Ginsberg, 1990; Klingel, 1974; Rowen, 1992). There is no specific anti-predator behaviour (Klingel, 1974), making the foals vulnerable to predation. Further, it is thought that foals are energetically constrained (Rubenstein, 1986; Williams, 1998b), and foal survival has been related to the distance that mothers move to water (Williams, 1998b).

1.2.3. Implications for this study

Any range-wide survey of Grevy's zebra must take the lessons from previous work, and the ecology and social behaviour of Grevy's zebra into account. It should cover all populations in as short a time period as possible. It would be best conducted in the dry season when zebra are constrained to permanent water sources and are unlikely to be ranging widely, particularly in the northern areas where the populations are believed to be at a far lower density and where resources, particularly water, are more limiting. Different reproductive classes of zebra will more likely be confined to areas where their particular resource priority is most abundant. It must not only survey the areas where zebra are found, but also local areas around these populations. As pastoralists range widely throughout northern Kenya it should also take local knowledge into account to identify areas where zebra are seen, and to identify the water sources that these populations use. Water is probably the most important factor affecting Grevy's zebra distribution. Hence the priority of any successful survey is to identify the resources that the populations will be using and will be limited by.

The social system of Grevy's zebra makes it likely that territorial males and lactating females will remain in an area even once the resources have become limiting and other more mobile reproductive classes are moving more widely (Ginsberg, 1989; Klingel, 1974; Rubenstein & Hack, in press; Williams, 1998b). They are also likely to be more faithful to specific locales where some resources remain, but when other classes of zebra are ranging more widely. Hence they are more likely to be resighted over the course of a multi-day CMR survey and thus may be over-represented. The assumptions of these models and the potential biases associated with using them to estimate Grevy's zebra population numbers will be dealt with in Chapter 3.

Finally, it is important to note that the previous long-term studies of Grevy's zebra have all occurred in the same population, where approximately 1000 individuals, each with unique stripe patterns, have been monitored using individual identifications over a period of ten years (Ginsberg, 1988; Rowen, 1992; Rubenstein, 1989; Williams, 1998b). Thus we can reliably assume that each unique stripe pattern represents a different animal in the population.

2. Study area: Regional overview, survey areas selection and descriptions

2.1 Regional overview

In general, northern Kenya is climatically characterised by a gradient of increasing temperature and aridity from south to north. North of Mount Kenya and the Tana River a semi-arid to arid plain stretches west to the Rift Valley, east into Somalia and north into southern Ethiopia. This region is the historical range of Grevy's zebra in northern Kenya (Fig. 1.1). The altitude ranges from 1800m a.s.l. in the south to 400m a.s.l. in the north. It is interspersed with relic lava flows that rise 50 – 150m above the surrounding plain. The area is vegetationally diverse, generally conforming to Pratt *et al.*'s (1966) Zones V (arid, with dry wooded or bushed grassland) and VI (very arid, with dwarf shrub grassland, dry bushed grassland, or barren land). Mean annual rainfall varies from 600mm in the south to 160-200mm in the north (Kenya Meteorological Department, 1984). Rain usually occurs in two seasons, March/April and October/November. Rain falls for shorter periods later in these seasons along the northerly gradient (Jätzold & Bake, 1995).

To the south-east of this plain the Laikipia plateau rises to altitudes of 1800 – 2600m. It conforms to Pratt *et al.*'s (1966) Zone V, but varies from dry wooded or bushed grassland to woodland and bushland. Mean annual rainfall throughout zebra range in Laikipia is 639mm (Georgiadis *et al.*, 2003).

2.2 Survey areas selection

The survey covered all areas where Grevy's zebra populations were known to exist. These areas were compiled from the most recent aerial surveys undertaken by the Kenya Wildlife Service (KWS) and DRSRS (Grunblatt *et al.*, 1996), and further substantiated from Wisbey's (1995) short survey (Table 2.1, Fig. 2.1). In addition, the survey sought to cover areas where anecdotal evidence described the existence of Grevy's zebra. For example, in Nairobi, anecdotes were collected from tour guides, other travellers, and missionaries who frequented the area (J. Sutton, H. Henley, R. Andersen, *pers. comm.*). Most importantly, once in the field, local knowledge from the pastoral people in each area was continually sought – not only within pre-selected areas, but throughout northern Kenya. This iterative process of information gathering resulted in 14 discrete areas being surveyed.

Threats to security prevented one large area, including Meru National Park and areas east (area A, Fig. 2.1), from being surveyed. However, 'guess-estimates' for this population were obtained from the warden's anti-poaching flights (M. Jenkins *pers. comm.*), and from the British Army Air Corps who were training in the area. Despite the size of the area (Fig. 2.1), this population was estimated to be very small.

2.3 Survey areas descriptions

The areas that were surveyed covered the climatic and environmental gradient described in section 2.1 above. They can be grouped into three broad eco-climatic regions (after Pratt *et al.*, 1966, see Table 2.1 and Fig. 2.1):

2.3.1 Region 1 – Arid dry wooded/bushed grassland (Areas 2 – 6, 10 and 12):

Area 2 was surveyed on five consecutive days. It is a wooded communal grazing area, with quite high densities of pastoralists. Water is available in a perennial river. The wooded nature of this area combined with the initial flightiness of the zebra made surveying more difficult.

Area 3 is the Buffalo Springs, Samburu and Shaba complex of national reserves, known to have high numbers of Grevy's zebra and no human activity. These reserves were surveyed for five consecutive days, followed by two re-supply days and then a further two consecutive survey days. Water is available in perennial rivers. The openness of this area, and the ability to get close to the zebra made this area easy to survey. However, the large numbers of zebra and the large group sizes made it unlikely that the whole area was surveyed completely every day.

Area 4 is a wooded communal grazing area that has one main perennial river, and was surveyed for five consecutive days. The zebra were typically found on open grassy areas in amongst the surrounding bushland. Pastoralists favoured these areas too, making the zebras timid.

Area 5 is a small area to the west of the perennial river in area 4. Occasional sightings of Grevy's zebra in this area were reported. It was surveyed completely in one day and only a few scattered groups found.

Area 6 is a communal grazing area with a high density of pastoralists. Water is found in springs which have human habitation close by. Except for small scattered groups, the majority of the zebra were found in large fluid groups in one small valley. This area was surveyed for two consecutive days, followed by two re-supply days and then four further survey days.

Area 10 is the large salt pan of Chew Bahir straddling the Kenyan-Ethiopian border. Bounded by rocky hills with bushed grassland, water is only available in springs. This is an area of ethnic human conflict where zebra are regularly hunted with automatic weapons. Their flight distance typically exceeds one kilometre, which combined with heat haze, makes it impossible to sex, let alone identify individuals. Three consecutive survey days were spent here.

Area 12 is largely bushed grassland utilised by pastoralists, where water is found in springs. Ethnic conflict had broken out here prior to our two consecutive survey days. Only small groups of zebra were seen.

Table 2.1: Areas surveyed, dates and number of survey days. Parentheses after number of days show breakdown of survey (s) & re-supply (r) days.

Area	Full name and location	Dates	# days
1.Lewa	Lewa Wildlife Conservancy	22/1 – 27/1	6 (6s)
2.LMD	LMD area north of Lewa	29/2 – 02/2	5 (5s)
3.Bs,S,Sh	Buffalo, Samburu & Shaba National Reserves	05/2 – 13/2	7 (5s+2r+2s)
4.Long	Longopita – Kipsing to Barsalinga	16/2 – 20/2	5 (5s)
5.Bars	Barsalinga – Barsalinga to Wamba	22/2	1 (1s)
6.Nagor	Nagor – West & south-west of Wamba	23/2 – 01/3	6 (2s+2r+4s)
7.Lais	All Laisamis surrounds incl. Logo-logo & Korr	04/3 – 10/3	7 (7s)
8.Karole	Southern tip of Chalbi desert	13/3 – 18/3	5 (2s+1r+2s)
9.Kala	Kalacha – eastern Chalbi desert incl. North Horr	19/3 – 20/3	2 (2s)
10.Seb	Sebarei & Chew Bahir	23/3 – 25/3	3 (3s)
11.Sib	Sibiloi National Park	28/3 – 31/3	3 (1s+1r+2s)
12.Bara	Baragoi – El Barta plains to Barsaloi	04/4 – 05/4	2 (2s)
13.S.Laik	Central Laikipia – Mpala, Ol Jogi, El Karama, Segera, Chololo	11/4 – 17/4	6 (1s+1r+5s)
14.N.Laik	N. Laikipia – Kisima, Mugie, Loisaba, Kirimun	19/4 – 24/4	6 (6s)
A	Kom-Merti-Garba Tula-Meru	N/A	N/A

2.3.2 Region 2 - Very arid dwarf shrub grassland, dry bushed grassland, or barren land (Areas 7-11):

Area 7 was surveyed for seven consecutive days. It is largely dry bushland, with water found in springs along the bases of relic larval ridges in the area. Except for one large fluid group of zebra found on grassland on top of a larval ridge, only small groups were occasionally seen. Pastoralists graze livestock in the areas around the springs.

Area 8 is the southern end of the Chalbi salt-pan as well as the larval hills to the east of the springs at Karole and Maydahat. The aridity of the area means that both Grevy's zebra and pastoralists with their livestock are widely dispersed. This area was surveyed for five consecutive days.

Area 9 surrounds the spring at Kalacha in the north-west of the Chalbi salt-pan, with the arid larval Huri Hills to the north–east. It was surveyed for two days.

Area 11 is made up of the arid larval hills to the west of Lake Turkana. Although mostly within Sibiloi National Park, this park only functions in a small radius around the park headquarters on the lake-shore. The rest of the park has high densities of livestock, and very low densities of wildlife. Grevy's zebra were found inland from the lakeshore. Despite extensive searching over three survey days, only one group was seen.

2.3.3 Region 3 - Arid dry wooded or bushed grassland to woodland and bushland (Areas 1, 13 and14):

Area 1 is a partially fenced wildlife conservancy that lies on the lower slopes of the Mt. Kenya escarpment. Water is found in perennial rivers. It was surveyed over six consecutive days. There are large numbers of Grevy's zebra in this area.

Area 13 is the central part of the Laikipia plateau. It is a large area, consisting almost entirely of cattle ranches where wildlife, particularly Grevy's zebra, are tolerated, and often encouraged – with some ranches engaging in tourist related activities. Water is found in perennial rivers and at artificial water-points. This area was surveyed for one day, followed by a re-supply day, and then five further consecutive survey days.

Area 14 is the northern part of the Laikipia plateau, and is characteristically similar to Area 13 above. This area was surveyed over six consecutive days.

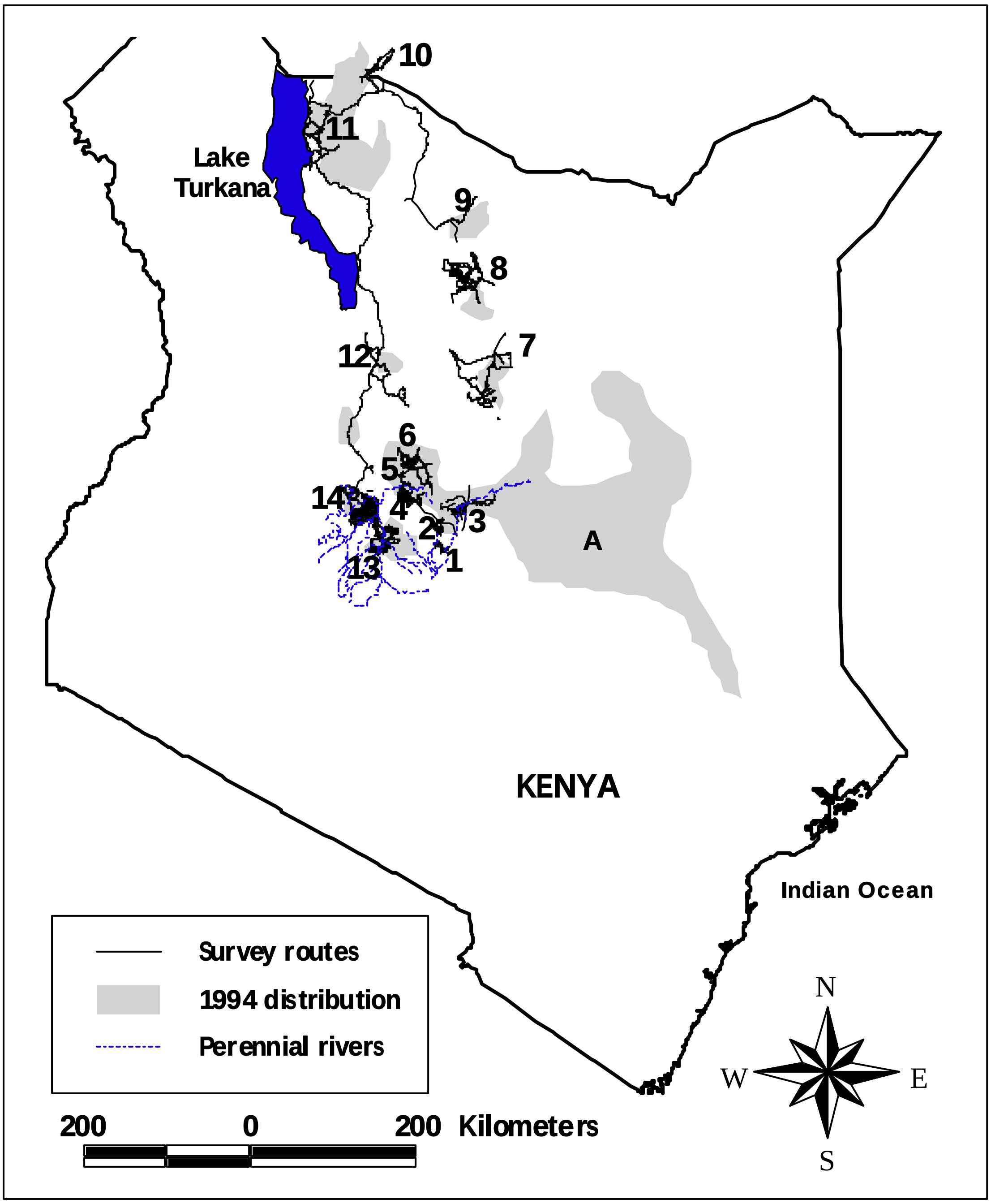

Figure 2.1: The 1994 distribution of Grevy's zebra in northern Kenya, with this survey's track routes, numbered survey areas (see Table 2.1) and perennial rivers. 1994 distribution from DRSRS surveys (Grunblatt *et al.*, 1996; Williams, 2002).

3. Estimating Grevy’s zebra population sizes using capture-mark-recapture (CMR) techniques

3.1 Introduction

Grevy’s zebra have undergone one of the most dramatic reductions in range of any African mammal in the last century, and their numbers are thought to have declined by 70% throughout their range (Rowen & Ginsberg, 1992; Williams, 2002). In addition recent work in northern Kenya has suggested that their numbers continue to decline due to competition with pastoral people and their livestock, and because of habitat change resulting from the long term effects of heavy sustained use of rangelands by domestic livestock (Williams, 1998b).

While relatively accurate estimates of population size resulting from long-term research projects are available for a few areas in northern Kenya (Lewa Wildlife Conservancy, Buffalo Springs and Samburu National Reserves), data for the majority of their range are non-existent or extremely poor. A short survey in the mid-90’s suggested that outside of the protected areas mentioned above Grevy’s zebra populations have become small and fragmented (Wisbey, 1995). Data from the Kenyan Department of Resource Surveys and Remote Sensing (DRSRS) support the continuing decline, although these data are collated from sample aerial surveys which have high standard errors and have proven to be unreliable for a low density, widely dispersed species such as Grevy’s zebra (see section 1.2.1, Grunblatt *et al.*, 1996; Muchoki, 2000; Williams, 2002).

The primary aim of this study was to provide an accurate population estimate for all populations of Grevy’s zebra throughout their northern Kenyan range. A ground survey using modified mark-recapture techniques was considered judicious (Rowen & Ginsberg, 1992) given the established inaccuracy of previous aerial survey work (Williams, 2002, see section 1.2.1), a proven system for recognising individual zebra from their stripe patterns (Ginsberg, 1988; Rowen, 1992; Williams, 1998b, see section 1.2.3), and the means to completely cover a manageably sized survey area repeatedly.

The specific objectives were:

1. to improve the accuracy of previous estimates based on aerial surveys,
2. to provide reliable estimates and distribution data for previously unsurveyed populations,
3. and to assess the current population trend against the previously available estimates.

3.2 Methods

Mark-recapture population estimation models are based on two basic assumptions that are often not met in field studies (Krebs, 1999; Otis *et al.*, 1978; Pollock *et al.*, 1990). These are that:

1. all animals are equally likely to be caught in each sample, and that
2. marks are neither lost nor inaccurately recorded.

Equal catchability can be influenced by three recognised sources of variation (see section 1.1.1.1, Nichols, 1992; Otis *et al.*, 1978): heterogeneity, behavioural responses and time.

The behavioural ecology of Grevy's zebra suggests that there could be variation in 'catchability'. Firstly, individual differences in behaviour resulting from reproductive status could lead to both heterogeneity in catchability, and behavioural biases in catchability. For example, the restricted spatial distribution of territorial males and lactating females is likely to make them easier to resight. To overcome this, the areas containing resources that all reproductive classes will require must be found and surveyed each day – i.e. not only water but also foraging areas further from water.

Secondly, populations that live sympatrically with pastoralists are likely to be more wary than those in protected areas, though it is possible that they may become habituated to vehicles and hence more catchable over time. This would appear as either a temporal or a behavioural bias, or a combination of both. This can best be overcome by diligently trying to photograph all zebra each day, especially early in a survey before any possible habituation has occurred. However, as the time spent photographing individual zebra decreases over a survey period, the area is likely to be searched better over time, presenting another possible bias that might appear as variation in time and/or behaviour.

These possible biases could be further compounded by low density populations, where individuals whose reproductive status makes them more faithful to specific resources might be more easily found than those who range widely in search of more distributed resources – especially with possible home range sizes of 10000km^2 (Ginsberg, 1988). Exploration of the survey areas to delimit the size of the overall area to be surveyed would allow them to be searched as meticulously as possible, and increase the probability of sighting animals that were more difficult to see either at the beginning of a survey before habituation occurred, or because of their reproductive status (see section 3.2.1 below).

It is worth noting that mathematical models have been developed to compensate for bias in catchability when it is found within a dataset (see section 3.2.3.2). However, failure of the second assumption (see below) cannot be accounted for *post hoc*.

Failure of the second assumption (marks are neither lost nor inaccurately recorded) is highly unlikely in this study – the natural markings used did not change over the short time periods of the surveys (see section 1.2.3). However, poor quality images are a potential source of bias (Forcada & Aguilar, 2000; Gowans & Whitehead, 2001; Stevick *et al.*, 2001) and must be excluded. Moreover each possible match must be checked rigorously (see section 3.2.3.1 below).

3.2.1 Data collection

The survey was conducted between 19 January and 24 April 2000 – i.e. during the mid-late dry season when zebra would be more constrained by water distribution. Small amounts of rain fell in three of the areas, but each rainfall was insufficient for ephemeral water sources to form and hence affect the distribution of zebra relative to permanent water sources.

The survey was carried out using vehicles and a team of volunteers. The volunteers were given five days training in the first area – which is an area where Grevy's zebra are found in high density, are habituated, and hence easy to sex and photograph.

In each area, at least one day was initially spent using local knowledge to confirm the presence of Grevy's zebra, to identify the water sources they were using, and to investigate any other resources within the wider area – typically up to 20km from the nearest water. With this knowledge, the survey areas were delimited beyond all resources and areas where zebra were known to occur.

Areas were then surveyed intensively for Grevy's zebra for a minimum of five days. Low density areas or areas that were wholly inaccessible because of the terrain were surveyed for shorter periods. Where possible survey days were consecutive, but occasionally for logistic reasons this was impossible; survey periods never extended beyond a total of ten days (see Table 2.1).

Because of the large size of the areas three vehicles were used. Each area was split into sections such that each section could be surveyed entirely by one vehicle in one day (three for all except the last two areas, 13 and 14, which were split into four sections as an extra vehicle was available).

Each day, each vehicle searched completely an entire section, both on and off roads. The sections were searched from one end (normally that nearest a road) to the other. Thickets and broken terrain that were difficult to access were also searched meticulously. The objective was to find every zebra in each section every day.

For each zebra group sighted, data on location, group size and structure were recorded (see Chapter 4). The right rear side only of as many Grevy's zebra as possible were photographed using standard SLR cameras with 500mm mirror lenses and 100 ISO black and white negative film. Care was taken to approach and attempt to photograph all animals seen, even those that were initially wary.

The maximum number of zebra seen each day (where any groups or individuals that were possible resightings were excluded) was recorded daily such that the maximum number seen on one day in each area could be used as a minimum estimate for the area.

3.2.3 Data analysis

3.2.3.1 Cataloguing and 'striping' for individual identification

Exposed films were developed into negatives and then individually scanned at maximum resolution (2700dpi using a CanoScan FS2710 negative scanner) to preserve stripe information. The digital images were then cropped to include just the area used to identify the zebras, hence reducing file size. When more than one zebra was photographed in a single image it was split to create one individual per image. Each image was coded by film, negative number, area and date so that all digital files could be related back to the original negative.

The digital images were then catalogued into Portfolio 4.1, a digital image cataloguing application (Extensis, 1999). The quality of each image was then assessed by judging whether it was possible to identify five or more stripes in the upper thigh region (i.e. out of the first ten stripes from the level of the anus down). Poor quality images were excluded. Poor quality images could result from increased distance, bad light, vegetation or other animals obscuring stripes, the photograph having been taken with the zebra at an angle from which the stripes could not be read, or bad photography. The inclusion of poor quality images can bias results by matches being missed, either on the same or different days.

Searchable keywords were attributed to each image. These included the area in which the image was taken, the date the image was taken, the reproductive condition of the zebra, any unique identifiers (e.g. rare stripe configurations, scars or missing tails), and the coded stripe pattern.

The technique for coding and individually identifying Grevy's zebra from their right rear thigh stripe pattern is well established and has been successfully used in five previous studies (Ginsberg, 1989; Rowen, 1992; Rubenstein, 1986; Williams, 1998b; Wisbey, 1995). The stripe patterns are classified into six distinct shapes (Y [y], bar [b], vee [v], chromosome [c], eye [e], and dash [d]; Fig. 3.1). The stripes are then read from as near to the top of the right rear thigh as possible, and as far down to the hock as possible. In this way each animal is assigned a unique stripe code, (e.g. in Fig. 3.1 the code is vvedcvdybbybdeyybvyyb).

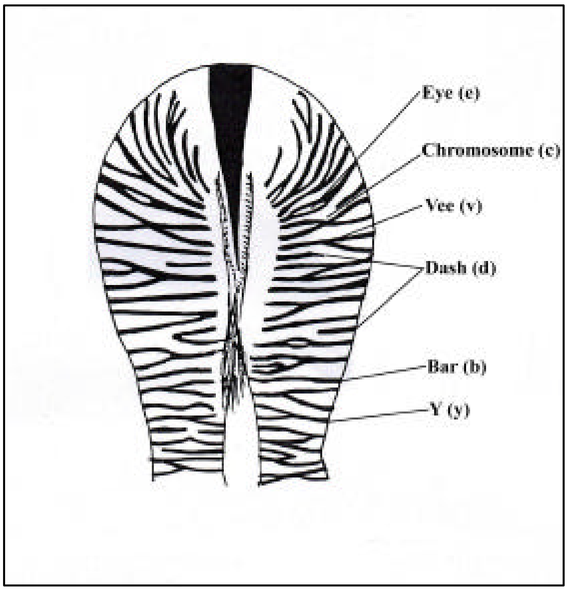

Figure 3.1: Grevy's zebra stripe pattern coding convention.

Portfolio allows a number of different stripe codes to be assigned to a single individual. Therefore images where the zebra was at a slight angle and it was impossible to judge exactly what the stripe code would be if you were seeing it directly from behind could be included by assigning all possible stripe codes. Although experience helps in assigning stripe codes, the ability to assign numerous stripe codes to an image allows even inexperienced people to follow the same rules and find the same matches.

The database was then searched for matching keywords, or, in the case of the stripe codes, parts of keywords to identify potential repeat sightings of the same individual on the same or different days. Matches were displayed in a new viewing gallery and each possible match was then assessed visually to confirm matches that were resightings of the same individual. Repeat sightings of the same individual on the same day were excluded.

3.2.3.2 Population size estimation models

Three methods were used for population estimation. Firstly, given that model-based estimators typically require a minimum of n = 25 different individuals (Otis *et al.*, 1978; White *et al.*, 1982), in areas where less than 25 different zebra were sighted, minimum population estimates were made from the maximum number of individuals counted in the field on a given day. Any groups that were possible resightings on the same day were excluded from these estimates. Secondly, given the possibility of bias in equal catchability that the behavioural ecology and local conditions in northern Kenya suggest (see section 3.2 above), the population estimation models selected needed to be robust enough to test for and incorporate bias. For this reason Program CAPTURE (Rexstad & Burnham, 1991; White, 1982; White *et al.*, 1982) and Bowden & Kufeld's (1995) resight model for telemetry data were chosen.

CAPTURE requires demographic closure of the population, and ideally a minimum of five sample periods (Rexstad & Burnham, 1991). The survey periods of five to ten days allowed the assumption of closure to be met (Otis *et al.*, 1978). CAPTURE contains mathematical models that have been developed to account for the different sources of variation in capture probability. Some of the combination models (e.g. M_{th} – time and heterogeneity model) are so general, and thus have so many parameters, that they become harder to fit to observed data and hence estimation of population size is difficult (Seber, 1986; Young & Young, 1998). In particular, it is difficult to distinguish temporal from other sources of variation (Lancia *et al.*, 1996), and at present the full model M_{tbh} remains unsolved. CAPTURE computes goodness-of-fit statistics, between-model test statistics and infers which sources of variation in capture probabilities are important for a given data set (Rexstad & Burnham, 1991; White *et al.*, 1982). However, model selection procedures within CAPTURE have low power for small populations (Menkens & Anderson, 1988), and where possible, biological information should be used to reduce the number of reasonable models (Rexstad & Burnham, 1991).

When the bias in catchability resulted in models that were irresolvable within CAPTURE, or which were so general that the estimates had a large standard error, Bowden and Kufeld’s (1995) model, developed for population estimation from radio-telemetry data, was used. This model allows the assumption of equal catchability (and hence closure) to be relaxed – the trade-off being wider confidence intervals (Krebs, 1999). Sightings from day one were used as the marked (‘tagged’) animals and the frequencies of sightings of these individuals within the population over the rest of the survey were used to estimate N and the 95% confidence interval (White, 1996a). This model was run from within Program NOREMARK (White, 1996b, c).

However, this model requires the distribution of sighting probabilities to be the same for both marked and unmarked animals (White & Shenk, 2001) – hence, if heterogeneity within the population is known to exist, the number of marked animals (i.e. animals seen on day one) must be large and selected as randomly as possible.

Encounter histories were deduced for each individual identified in each area by recording whether they were seen or not each day (0 = absent; 1 = present). Illustrated with an example of five animals from area 3:

BS001F	1101100
BS002F	1101100
BS003F	0110100
BS004F	0110100
BS005F	0011110

The encounter histories for all individuals indentified in an area were then amalgamated for input into the population estimation software.

The encounter histories for each area were first tested for equal catchability among individuals with the Zero-truncated Poisson test (Chi-square goodness-of-fit test, Caughley, 1977; Krebs, 1999). This test is appropriate when the time period between the first and last samples is short enough to ensure negligible mortality (Caughley, 1977; Krebs, 1999). It is therefore applicable to this study: no mortality was recorded over the course of the surveys of the areas.

Encounter histories from the areas with suitable sample sizes were then run through CAPTURE's model selection process to select the models with best fit for each data set. CAPTURE uses probability theory to compare the likelihood of the encounter histories under the different models of capture behaviour. The appropriate models were then used to estimate population size (N) with a 95% confidence interval. Where CAPTURE was unable to select a model, or where the model selected was unreliable, Bowden and Kufeld's model was run from within NOREMARK (White, 1996b, c).

As an important objective of this exercise was to generate an overall population estimate across all the areas in northern Kenya, the absence of confidence intervals for some areas (where estimates are based on maximum number seen) was problematical. The following mathematical strategy was used to provide estimates of the confidence intervals for these problem areas – the variance from the areas where models could be run was regressed against the estimates of N from the remaining areas, and values for the variance of the minimum number estimates were then interpolated. The estimates provided a good prediction of variance: $R^2 = 0.771$; $V = -32.8+2.05(N)$. For minimum estimates where $N < 25$ the interpolated variances approached zero, and these areas were all given the same variance as $N = 26$.

The overall estimate for the population of Grevy's zebra in northern Kenya was then obtained by summing the estimates from the CMR models, the minimum estimates from the remaining survey areas, and the 'guess-estimates' from the low density eastern area (area A). Confidence limits for this estimate were obtained by summing the variances across these estimates (including those interpolated variances from the minimum number estimates and the 'guess-estimate'), then applying the additive property of variances (i.e. the variance of a sum is equal to the sum of the variances, Sokal & Rohlf, 1995) the 95% confidence interval from the standard error of the overall estimate was derived.

3.3 Results

A total of 10448 cropped images resulted, 6322 of which were of acceptable quality to be included in the analyses (Table 3.1). The number of animals individually identified in each population after recapture matching provides a minimum estimate for the populations (Table 3.1).

In five areas (5, 9, 10, 11, and 12; as well as area A – see Table 2.1) insufficient zebra were sighted to warrant running CMR estimation models, while in area 7, the zebra were found in inaccessible terrain. These populations were extremely difficult to photograph, either because of inaccessible terrain, or because they were extremely skittish. In practice there were very few zebra in these areas, making the groups easily recognisable in the field – from group structure and location. This allowed the estimation of the minimum number of zebra for these areas (from the maximum number seen on one day; see Table 3.3).

Table 3.1: The number of cropped images, good quality images and individuals identified by area.

Area	# cropped images	# quality images	# individuals ID'd
1.Lewa	2671	1787	549
2.LMD	444	254	75
3.Bs,S,Sh	2248	1756	562
4.Long	527	367	97
5.Bars	35	19	13
6.Nagor	1693	908	218
7.Lais	390	68	35
8.Karole	334	57	36
9.Kala	0	0	0
10.Seb	0	0	0
11.Sib	48	5	2
12.Bara	31	6	3
13.S.Laik	1172	734	166
14.N.Laik	855	361	162
Totals:	**10448**	**6322**	**1918**

Encounter histories from the remaining eight populations were created to be analysed with recapture or resight models. The null hypothesis of equal catchability was rejected for seven of these eight populations (1-4, 6, 13 and 14) using the Zero-truncated Poisson test ($\chi^2 = 12.381$; d.f. = 5; $P < 0.05$). The only area where it could not be rejected was area 8 ($\chi^2 = 0.83$, d.f. = 3, NS). These results were anticipated from sources of possible bias noted in the field (discussed in section 3.2 above).

The bias was of particular concern in areas 1 and 3 – which were the only two effective protected areas surveyed – where zebra were found in the greatest numbers (Table 3.3) and highest densities. In these two areas zebra were distributed more widely than in areas where they were found in sympatry with livestock and where they were found to occupy smaller ranges (see section 4.3, Table 4.3).

Initial model selection in CAPTURE bore this out. Model M_{tbh} (which is irresolvable) was selected for area 3 – with no other model being scored highly enough to be selected as an alternative, while for area 1 model M_{tb} was selected, but model M_{th} was almost indistinguishable, again suggesting bias in time, heterogeneity and behaviour.

In addition the low capture rate and, therefore, capture probability of zebra in area 8 meant that no model could be selected and it was excluded from this analysis.

In the remaing seven areas, model selection within CAPTURE was run resulting in population estimates with 95% confidence intervals (Table 3.2).

Table 3.2: Population estimates with standard errors and 95% confidence intervals from Program CAPTURE. For models selected t=time, b=behaviour, h=heterogeneity; interaction models are shown as products.

Area	Model	Estimate of N	SE	Lower 95%	Upper 95%
1.Lewa	M_{tb}	1213	563.75	706	3362
2.LMD	M_h	105	10.49	91	133
3.Bs,S,Sh	M_{tbh}	Irresolvable	N/A	N/A	N/A
4.Long	M_{th}	157	22.16	127	217
6.Nagor	M_{bh}	358	27.93	313	422
13.S.Laik	M_{th}	213	13.64	194	248
14.N.Laik	M_{tb}	194	15.07	176	239

The biases in catchability in area 1 resulted in an estimate with high standard error (Table 3.2). This suggests that the population being sampled was not closed, although the area might have been geographically closed – i.e. the whole population was not able to be surveyed completely every day. However, the high density of zebra in this area and in area 3 meant that there were a large number of sightings on day one. These could then be used as the marked animals whose frequency of sighting within the population as a whole could be used to estimate N and its confidence limits with Bowden & Kufeld's (1995) resight model – which allows unequal catchability (see Table 3.3). In the absence of anything other than a minimum number estimate (N = 62) for area 8, this model was also used in order to estimate the standard error about the population estimate (Table 3.3).

The summation of the results led to an overall estimate for Grevy's zebra in northern Kenya – incorporating the minimum number estimates (areas 5, 7, 9-12), the CAPTURE estimates from areas 2, 4, 6, 13 and 14 (from Table 3.2), the Bowden estimates from areas 1, 3 and 8, and the 'guess-estimate' from area A (Meru and east). The estimates for each population show that the southern areas (areas 1-6, 13, 14 and Area A, see Fig. 2.1) hold the vast majority (87%) of the overall population – 2239 animals. The remaining six populations in the north of the Kenyan range are small and potentially isolated (see Fig. 2.1).

Table 3.3: Population estimates with 95% confidence intervals for all known populations of Grevy's zebra in northern Kenya. ID = individually identified animals; * = same model as used in Table 3.2.

Area	ID	Model	Estimate of N	SE	Lower	Upper
1.Lewa	549	Bowden	536	27.14	485	592
2.LMD	75	M_h*	105	10.49	91	133
3.Bs,S,Sh	562	Bowden	603	38.83	531	685
4.Long	97	M_{th}*	157	22.16	127	217
5.Bars	13	Min Est	13	20.5	4	22
6.Nagor	218	M_{bh}*	358	27.93	313	422
7.Lais	35	Min Est	101	13.20	75	127
8.Karole	36	Bowden	66	16.33	39	110
9.Kala	0	Min Est	30	5.36	19	41
10.Seb	0	Min Est	93	12.56	68	118
11.Sib	2	Min Est	16	20.5	7	25
12.Bara	3	Min Est	26	20.5	17	35
13.S.Laik	166	M_{th}*	213	13.64	194	248
14.N.Laik	162	M_{tb}*	194	15.07	176	239
Area A	0	Guess	60	9.50	41	79
Totals:	**1918**		**2571**	**69.41**	**2435**	**2707**

3.4 Discussion

This survey provides the most reliable estimate of Grevy's zebra numbers in northern Kenya to date, with narrow confidence limits. The confidence intervals are also far tighter than any achieved with the sample aerial counts.

Importantly, 1918 of the estimated 2571 (74%) zebra in northern Kenya have been identified and have stored images available for future reference (Table 3.3). This resource will assist population monitoring, as well as allowing important questions of movement and dispersal to be investigated.

Given the established inaccuracy of all previous population estimates this study has produced a reliable estimate against which future trends can now be evaluated. Possibly even more importantly, there are now current estimates and distribution data for each population of zebra. These will permit trends of individual populations to be monitored, allowing hypotheses regarding mechanisms driving declines or increases to be tested by comparative studies.

However, it is important to note that this should be recognised as a minimum estimate – in five survey areas only minimum estimates from the maximum number of individuals seen on a day were used (representing 12.6% of the total population estimate). In order to combine these estimates with those more rigorously derived from statistical techniques (and given that daily survey intensity for all areas was equal), a regression technique was used to acquire confidence limits for these minimum number estimates (see section 3.2.3.2).

Analysis of the data revealed limitations associated with the assumption of equal catchability. Although this was accounted for by selecting models appropriately, future results could be improved by further increasing sampling intensity. Increased sampling intensity would limit bias in catchability, hence allowing each population to be treated as a closed population. Thus appropriate models, which typically have a lower standard error about the estimates, could be run from within CAPTURE. This could be achieved either with extra teams on the ground – particularly in the protected areas with the large populations of zebra, or by spending more time establishing the exact whereabouts and movements of zebra populations within areas before starting to collect data, or both.

Further, the process of scanning, splitting, assessing for quality, coding and then matching each image was extremely laborious. The whole process took approximately 21 minutes per included image (6322 images), while the remaining 4126 excluded images took approximately 10 minutes to scan, split and assess for quality. This is a total of approximately 2901 hours, or 362 eight hour days! Using digital cameras would save approximately 871 hours, while automatic recognition software would save a further 842 hours. It is, however, advisable that the quality assessment and final matching are done by eye.

The final estimate represents a 40% decline from the 1992 estimate of 4300 animals (Rowen & Ginsberg, 1992) – although this estimate was based on guesses for many populations and has no overall confidence limits. The previously suggested fragmentation of the northern populations has also been established – these populations are particularly small and isolated. The loss of the northern populations would represent a significant overall range reduction, with an associated loss of inherent diversity.

4. The effects of livestock on Grevy's zebra recruitment and social structure

4.1 Introduction

While social behaviour in ungulates is strongly related to their ecology (Jarman, 1974; Rubenstein, 1986), heterogeneity of resource availability, competition, predation, and human-wildlife conflict (which effectively operates as competition, and/or predation), are all postulated to affect the local populations of large herbivores in Africa (Dublin *et al.*, 1990; Fritz *et al.*, 1996; McNaughton & Georgiadis, 1986; Olff *et al.*, 2002; Sinclair, 1985). In semi-arid and arid rangelands, water availability has been shown to be of particular importance (Bergstrom & Skarpe, 1999; McNaughton & Georgiadis, 1986; Western, 1975).

In arid and semi-arid environments, livestock and humans are more water dependent than wildlife species that are adapted to local conditions (Voeten & Prins, 1999). Hence people and their livestock live closer to permanent water sources (Stoddart *et al.*, 1975). When the people remain in permanent or semi-permanent settlements (cf. 'traditional' pastoral livelihoods founded on transhumance), in the long-term there are negative effects on vegetation, and empirical evidence has shown that their presence directly disturbs wildlife distribution (Fritz *et al.*, 1996), density (Verlinden, 1997), recruitment (Williams, 1998b), and the distance that they are found from water (Bergstrom & Skarpe, 1999; de Leeuw *et al.*, 2001). Previous work on Grevy's zebra has reported a negative relationship between juvenile survival and the distances moved by their mothers (Rowen, 1992; Williams, 1998b). Such costs to wildlife populations predict that, all else being equal, the recruitment into Grevy's zebra populations will be lower in areas with high livestock density compared to areas with low livestock density.

The relationship between the ecology and social systems of ungulates (Jarman, 1974; Rubenstein, 1986) further predicts that ecological disturbance will affect social systems. While the effect of human activity on the behaviour of carnivores has been documented (Boydston *et al.*, 2003; Frank & Woodroffe, 2001; Sunquist & Sunquist, 2001), little is known of its effect on ungulate behaviour. This study provided an opportunity to investigate the effect of livestock density on aggregative and ranging behaviour in Grevy's zebra.

Previous work found that Grevy's zebra will range widely (up to 10000km2 for both sexes – Ginsberg, 1988), when conditions demand, in search of resources. Aggregations range from territorial males who are typically solitary, through more stable associations of lactating females, to large fluid groups of the more mobile classes (Ginsberg, 1989; Rubenstein & Hack, in press). Further, in a study of spatial and temporal patterns of resource use, Williams (1998b) concluded that Grevy's zebra compete for critical resources, particularly food and water, with pastoralists and their domestic livestock.

This predicts that, in areas with high livestock density, zebra will either be found in extremely low densities as they range widely for scarce resources, or they will be found at high densities in 'refugia' where patches of available resources are to be found. Further, if the former is occurring then aggregations would be expected to be more regular and at lower group sizes than those in areas with low livestock density; while for the latter, aggregations should also be more regular, but with relatively high group sizes than expected as more animals are congregated in a smaller area.

4.2 Methods

The survey concentrated on all areas in northern Kenya where populations of Grevy's zebra are known, or are believed, to exist (see Chapter 2 for a description of the survey areas and their selection). In addition, when surveying each area, all water sources were actively sought using local guides. Their positions were recorded and whether they were protected from wildlife or not (e.g. by a thorn 'boma'). Overnight waterhole watches were used to confirm that zebra used these water sources.

4.2.1 Data collection

Section 3.2.1 introduces the field data collection methods. During each daily survey, when a group of animals was encountered, the following data were collected: position using a GPS and the total number of individuals.

The composition of zebra groups were recorded by age and sex, and within the sexes reproductive status was classified. The sexes are easily distinguished, even at a distance. A female's reproductive status can also be assessed visually and by using the ages of foals up to one year, which is estimated from body size and coat colour (Rowen, 1992). Females were then assigned to one of five classes (Ginsberg, 1989; Rowen, 1992):

1. Late pregnancy (final trimester – within four months of parturition);
2. Early lactation (three months post-partum);
3. Mid-lactation (three – six months post-partum);
4. Late lactation (six – twelve months post-partum);
5. Non-reproductive (containing cycling oestrous and anoestrous females, and including females in early to mid-pregnancy).

Oestrus in females was recorded when observed. Oestrus was determined both morphologically (the presence of enlarged labia, vaginal 'winking' of the labia, tail position) and behaviourally (mounting by territorial males).

Territoriality in males is recognised in a variety of ways. Territorial males are generally larger than other males (Ginsberg, 1989), and they advertise with a characteristic bray and a distinctive upright posture. They also chase other males in a ritualistic fashion when in the presence of an oestrous female. If any of these characterising signals were observed, the male was classified as territorial. All other adult males were assumed to be bachelors.

During each daily survey distance driven (km) was recorded as a measure of search effort. This was preferable to a time-based measure because a large amount of time could be spent trying to photograph a group of zebra (for the mark-recapture population estimates, see Chapter 3), which was lost to searching. Photographing zebra might have involved driving, but these were relatively small distances, and when moving observers were continually looking for other zebra and livestock.

4.2.3 Data analysis

All analyses, unless otherwise indicated, were done using general linear models (GLM, Grafen & Hails, 2002; McCullagh & Nelder, 1987), allowing both categorical and continuous predictors to be included. Al analyses were done using Minitab, release 13.31 (Minitab, 2003).

4.2.3.1 Livestock densities

Analyses used areas as the appropriate units of comparison on the grounds that livestock densities were obtained from the sum of the total number of animals seen over the whole survey in each area divided by the total distance driven. Hence livestock densities are expressed in animals encountered per driven km for each area.

4.2.3.2 Distance to water

All location data for groups of animals and water points were entered into a GIS (ArcView 3.2, ESRI, 1999). The distance of all zebra groups to the nearest ‘usable’ water was then extracted. Because wildlife is excluded from numerous water points, either purposefully by humans or by the nature of the access to water (where bushiness and slope determine the visibility and accessibility to the water, Ginsberg, 1988), only those points to which wildlife had access were included in the analyses. In the few places where rivers were perennial, the stretches that contained water were entered into the GIS and shortest distance to the river was used.

4.2.3.3 Recruitment

Recruitment was measured by the proportion of all adult females that were lactating. Total adult females were used to standardise across populations rather than all adults as adult males make different decisions regarding dispersal and habitat suitability than do females (see section 1.2.2, Ginsberg, 1989). Female zebra with foals of 0-6 months (i.e. early and mid lactation females) were assumed to be lactating following Rowen's (1992) findings that weaning begins at six months.

4.2.3.4 Social behaviour

First, the use of space within each survey area was examined with kernel home range estimates (Worton, 1989). The area containing 95% of sightings of zebra groups was calculated using the Spatial Analyst 1.1 extension within ArcView 3.2 (ESRI, 1999). The effect of livestock density on the size of this area was then investigated using the different areas as replicates (the null hypothesis being that zebra 95% kernels were unaffected by livestock density).

Second, the level of dispersion among groups of zebra was determined using an index of dispersion. Dispersion in this context can be visualised as the degree of 'clumping' exhibited by the populations in each area. For a given population size, clumping is at a minimum where group sizes are the same (extreme under-dispersion) and at a maximum where all individuals are observed in the same sampling unit (extreme over-dispersion). The midpoint of this index implies that group sizes distributions are consistent with a Poisson (random) distribution.

Green’s coefficient of dispersion (see equation below, where x is the mean group size by day by area, and $\bar{x}$ the overall mean group size by area) is an index based on the variance to mean ratio:

$$\frac{(s^2/\bar{x})-1}{\sum x-1}$$

Green’s index was chosen because it is independent of variation in the number of sampling units, the sample mean, and the total numbers in the sample. It ranges from zero for random dispersion to one for maximum contagion (Elliott, 1977). Where distributions are more regular than random the index is negative. Although Green (1966 in Elliott, 1977) suggests that it should not be used when the number of samples < 50, Elliott (1977) believes this to be unduly “pessimistic”. While this condition is not always satisfied here, the primary aim is not to determine a ‘true’ value for any site but to compare dispersion among the sites.

Green’s coefficient was calculated for zebra on each day for each area. Analyses were then conducted using this daily index of dispersion as the response variable. While the arcsine transformation is frequently appropriate for a response constrained between limits (Krebs, 1999), this index was not transformed as a scrutiny of residuals suggested no deviations from GLM assumptions. Daily values accounted for the fluid associations of some of the reproductive classes of Grevy’s zebra – whose associations can change daily (Ginsberg, 1989; Klingel, 1974; Rubenstein & Hack, in press).

Finally, group size among areas was investigated as a response variable.

4.3 Results

Of the 14 areas surveyed, five areas were omitted from all analyses. In area 9 (see Chapter 2) survey work had focussed on interviews and overnight waterhole watches (when Grevy’s zebra were heard), which confirmed the presence of zebra despite none being seen. In three other areas the numbers of zebra classified into reproductive classes were too small to warrant inclusion (5: n = 6; 11: n = 3; 12: n = 9). While area 10 was excluded from the recruitment analyses because zebra were regularly hunted and could not be approached closely enough (flight distance was estimated to be >1km) to determine reproductive status (only 29% of individuals were classified; in contrast, the mean for all [including this] areas = 84%; S.E. = 5.20). The low sample size thus precluded it from the analyses on social behaviour (n = 37).

4.3.0.1 Livestock densities

Table 4.1 summarises the search effort, density and recruitment associated data for all areas surveyed.

Table 4.1: Population size estimates (from Table 3.3), total distance driven (km; search effort), total number of all livestock, livestock densities (animal per driven km), and the percentage of females that were lactating, by area.

Area	Pop est Gz	Effort (km)	Total lv	Lv density	%Lac fm
1.Lewa	536	856.4	0	0	13.3
2.LMD	105	910.3	10543	11.6	9.0
3.Bs,S,Sh	603	1623.3	3358	2.1	8.4
4.Long	157	923.2	6784	7.4	3.3
5.Bars*	13	297.8	3149	10.6	0
6.Nagor	358	1200.8	19411	16.2	3.5
7.Lais	101	1014.4	3747	3.7	4.4
8.Karole	66	1720.8	29702	17.3	4.2
10.Seb*	93	529.1	643	1.2	41.2
11.Sib*	16	1056.8	1745	1.7	0
12.Bara*	26	616.4	350	0.6	75.0
13.S.Laik	213	2233.4	8645	3.9	21.6
14.N.Laik	194	2208.3	13538	6.1	17.6

* excluded from all analyses – see above.

4.3.0.2 Distance to water

Fig. 4.1 shows the mean distance from ‘usable’ water sources of all groups of zebra, and lactating females for the areas used in these analyses (see above). All ‘usable’ water sources are shown in Fig. 5.1.

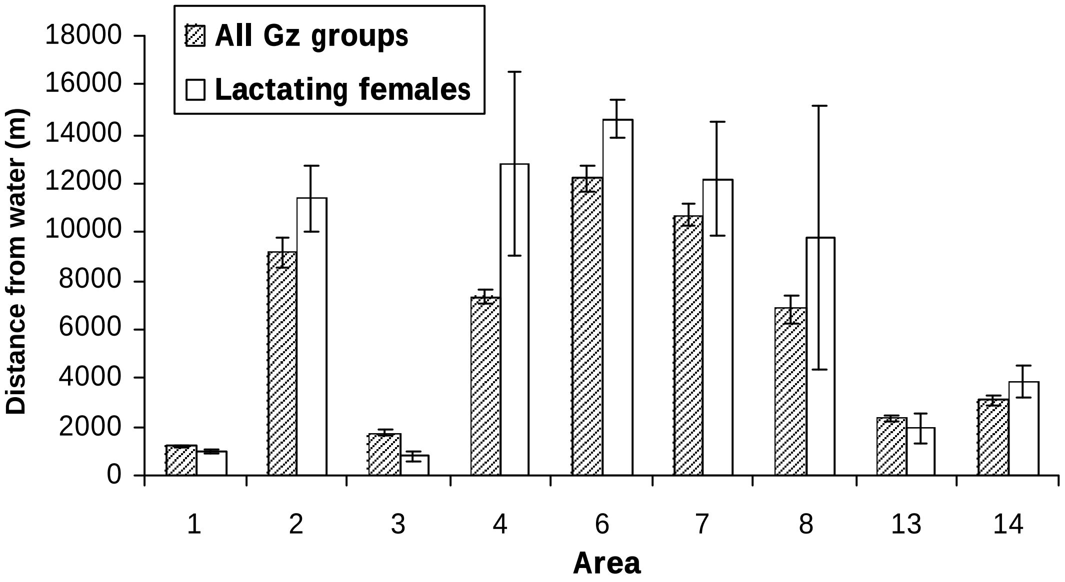

Figure 4.1: Mean distance from water of all groups of Grevy's zebra, and for all lactating females, by area – with standard error bars.

Inspection of Fig. 4.1 reveals that areas 1, 3, 13 and 14 are clustered with Grevy's zebra being found closer to water than the remaining areas. What is noteworthy is the different management approaches within the two different clusters of areas. In the cluster where zebra are found closer to water, areas 1 and 3 are protected areas, while areas 13 and 14 consist almost entirely of private ranches where Grevy's zebra are tolerated and even encouraged (see Chapter 2). The areas in the cluster where zebra are found further from water are all communal pastoralist grazing areas.

The effect of this was investigated with GLM models, using both the distance from water of all Grevy's zebra groups, and the distance from water of lactating females only, as response variables. The land management category was used as a binary categorical explanatory variable (where the levels are 'protected' and 'pastoral'). Both results were significant (All to water: $F_{1,7} = 36.02$; $P < 0.0025$; Lactating to water: $F_{1,7} = 87.43$; $P < 0.001$). Hence there is strong evidence that management approach affects the distance that Grevy's zebra are found from water (Fig. 4.2).

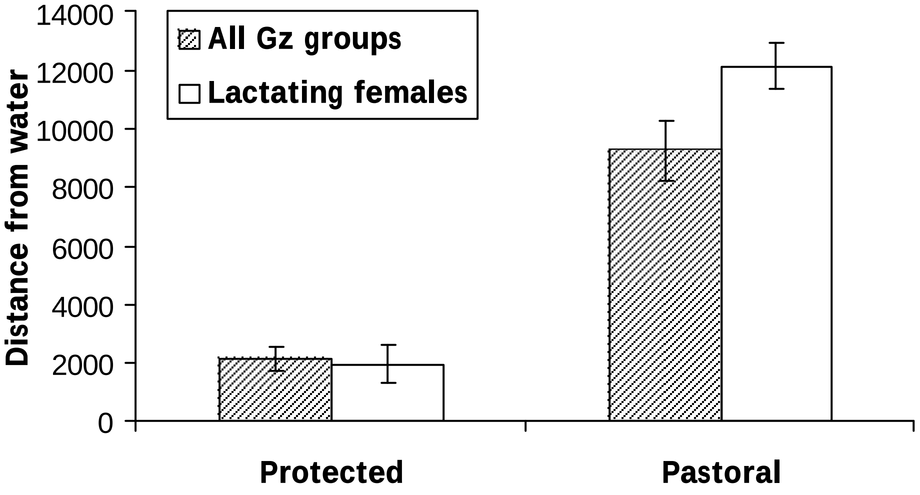

Figure 4.2: Mean distance from water of all groups of Grevy's zebra (P < 0.0025), and of all lactating females (P < 0.001), by management type – with standard error bars.

4.3.0.3 Recruitment

The percentages of lactating females for all areas are in Table 4.1 above, with the mean distances from water of lactating zebra by area in Fig. 4.1.

Preliminary investigation revealed that the distance that lactating females are found from water is positively correlated with livestock density (Pearson correlation coefficient = 0.692; $P < 0.05$). The same positive correlation was found for the distance all zebra groups to water (Pearson correlation coefficient = 0.657; NS) – although not statistically significant, the strength of the trend implies that it is biologically important. Finally, the distance that lactating females were found from water was negatively correlated with the percentage of lactating females (Pearson correlation coefficient = -0.760; $P < 0.05$).

The minimum adequate GLM model with the percentage of lactating females as the response variable included only the distance of lactating females from water ($F_{1,7} = 9.56$; $P < 0.025$) as the explanatory variable. A GLM model with management category as a binary variable, found this to be a predictor of the percentage of lactating females ($F_{1,7} = 14.06$; $P < 0.01$;

Fig. 4.3). Hence management category and distance from water are confounded (or non-orthogonal) predictors of percent lactating.

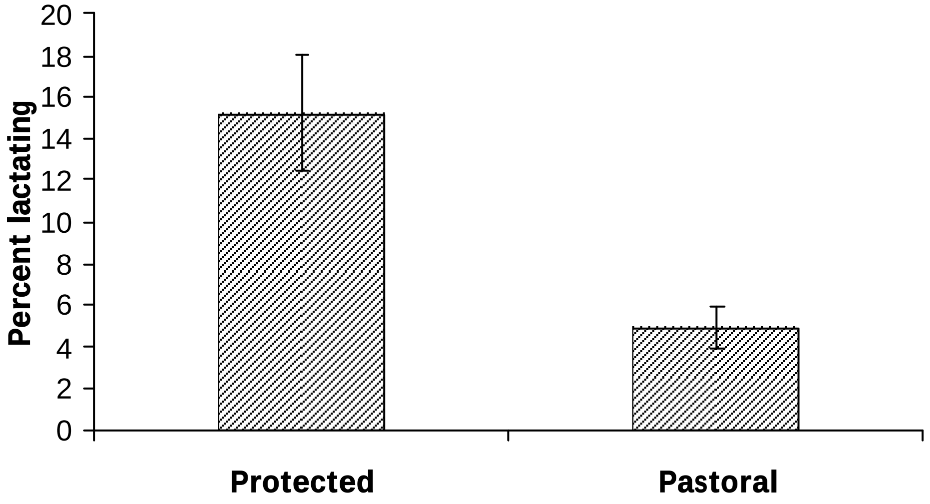

Figure 4.3: Percentage of lactating Grevy's zebra by management type (P < 0.01) – with standard error bars.

4.3.0.4 Social behaviour

Table 4.2 summarises the data used for the spatial distribution and aggregation analyses.

Table 4.2: 95% kernel sizes (km^2), population size estimates (Chapter 3), dispersion coefficients (Green's index), mean group size (with standard error) and mean distance from water (m; with standard error), by area.

Area	Kernel	Pop	Dispsn	Gpsize	SE	Gz dist	SE
1.Lewa	95.4	536	0.033	6.3	0.40	1236.51	50.39
2.LMD	73.9	105	0.154	4.6	0.89	9176.72	639.36
3.Bs,S,Sh	216.0	603	0.044	6.5	0.54	1757.86	111.07
4.Long	96.3	157	0.084	3.4	0.50	7377.30	292.33
6.Nagor	46.0	358	0.110	9.7	1.40	12202.85	506.17
7.Lais	80.9	101	0.075	6.9	1.01	10680.74	457.05
8.Karole	139.5	66	0.032	3.5	0.41	6844.41	610.09
13.S.Laik	100.8	213	0.041	5.3	0.48	2333.38	141.75
14.N.Laik	181.8	194	0.023	4.5	0.31	3126.34	175.00

The analyses of spatial distribution within survey areas confirmed that zebra distribution patterns are affected by distance from water. Kernel size is negatively correlated with distance from water (Pearson correlation coefficient = -0.667; P = 0.05). The minimum adequate GLM model only includes distance from water ($F_{1,7} = 5.61$; P = 0.05), thus equating to a linear regression (Fig. 4.4, Grafen & Hails, 2002). Kernel size was unrelated to population size (Pearson correlation coefficient = 0.324; NS). A GLM model showed that management type is not a predictor of kernel size ($F_{1,7} = 3.76$; NS).

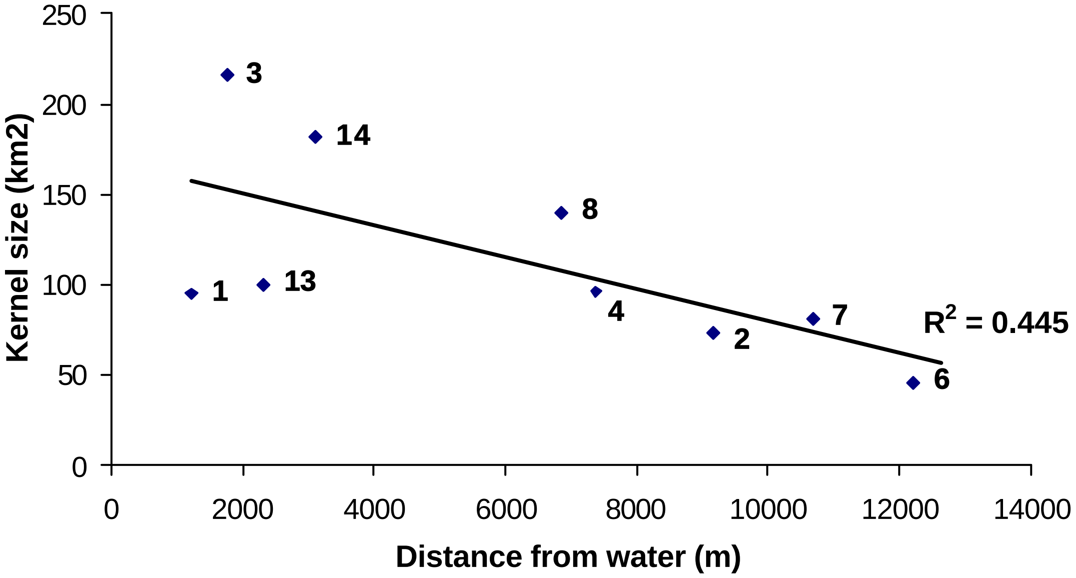

Figure 4.4: Linear regression of 95% kernel size (km²) against distance from water for Grevy's zebra (P = 0.05). Numbers cross-reference areas, see Table 4.2.

Green's coefficient of dispersion was found to be positively correlated with the distance that zebra are found from water (Pearson correlation coefficient = 0.734; P < 0.025). The minimum adequate GLM model included only distance of zebra from water ($F_{1,7} = 8.18$; P < 0.025). While dispersion was related to distance from water, inspection of the variance to mean ratios in each area on each day suggested that zebras were significantly aggregated (compared with random) most of the time (chi-square test [variance to mean ratio] for agreement with a Poisson series, Elliott, 1977, p.42). The GLM model of management category as a predictor of dispersion found the effect of the clustering to be significant ($F_{1,7}$ = 5.77; P < 0.05; Fig. 4.5).

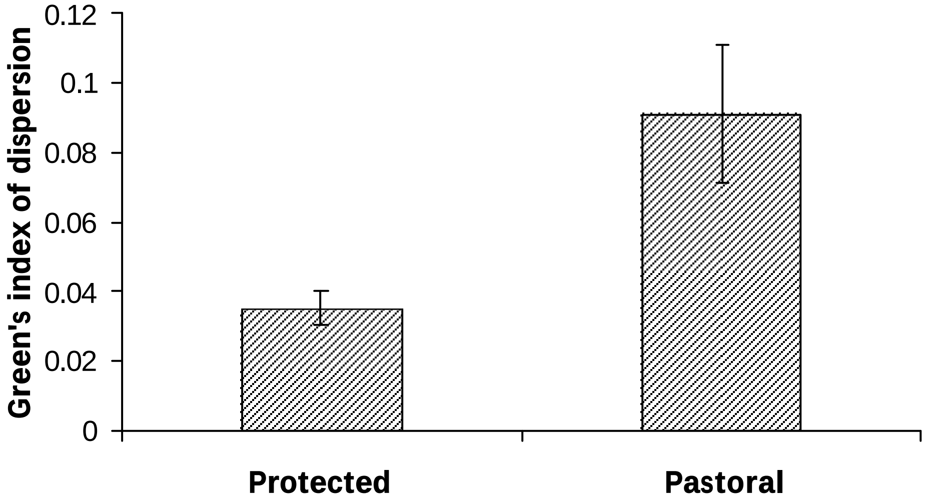

Figure 4.5: Green's index of dispersion by management type (P < 0.05) – with standard error bars.

Mean group size for each area was investigated, and the minimum adequate GLM model was found to include the mean distance from water of all zebra, the kernel size and an interaction between these two (Table 4.3). The mean group size increases significantly with distance from water, indicating that for large kernel sizes mean group size decreases with distance from water, while at small kernel sizes it increases. Given the relatively small sample size, this interaction may not be a robust effect.

Table 4.3: The minimum GLM model with the mean group size of Grevy's zebra by area as the response variable.

Parameters	Type III SS	d.f.	F	P	Coefficient
Mean distance water (all)	18.754	1	14.26	<0.025	0.00094
Kernel size	5.908	1	4.49	NS	
Dist water (all)*Kernel size	23.912	1	18.18	<0.01	-0.00001
Error	6.577	5			
Total	34.196	8			

4.4 Discussion

4.4.0.1 Recruitment

The results support the prediction that recruitment into Grevy's zebra populations will be lower in areas with high livestock density compared to areas with low livestock density. The distance that lactating females are found from water is significantly positively correlated with livestock density, while the further from water that lactating females are found, the significantly smaller percentage of the female population they constitute (section 4.3.0.3). However, this observed pattern does not infer causation. An alternative hypothesis might be that the populations with fewer lactating females are able to range further from water. But for this to hold, and given the water requirements of lactating females, and the fact that in populations with lower livestock densities they choose to be closer to water, we would expect to find lactating females closer to water than the mean for all zebras in these populations. This is not the case (section 4.3.0.3). Thus, the inference is that in populations that are found in sympatry with humans and their livestock, females are forced to live further from water which leads to a lower percentage of females with young foals from 0–6 months.

The cause of this decreased recruitment in populations living sympatrically with pastoralists and their livestock is not immediately apparent from this work. One hypothesis previously suggested relates juvenile survival to the amount their mother's move (Rowen, 1992; Williams, 1998b). Lactating female Grevy's zebra with foals aged 0-3 months must drink daily (Becker & Ginsberg, 1990; Ginsberg, 1989). They leave their foals in kindergartens (Becker & Ginsberg, 1990; Klingel, 1974; Rowen, 1992), where the lack of anti-predator behaviour (Klingel, 1974) makes them vulnerable to predation. This risk is magnified by Grevys zebra drinking nocturnally in pastoralist areas to avoid diurnal monopolisation of the water sources by people and their livestock (Williams, 1998b). The increased distance to water in these areas means that the foals will be susceptible to predation for long periods each night, whilst once they begin drinking water at 3 months (Becker & Ginsberg, 1990; Rowen, 1992) the long distances could place physiological stress on the foals.

This work raises a second hypothesis based on the apparent social effects of living further from water. The tendency of these populations to range less, to be more aggregated, and to be found in larger groups, might interfere with territoriality, and hence the mating system, and thus could lead to lower recruitment. Finally, given that Grevy's zebra females do not choose to live this far from water (cf. areas with decreased livestock where they are found closer to water), it is likely that females in these areas suffer physiological stress, and thus might well be less likely to come into oestrous.

Four specific areas were found to be extremely important for overall recruitment within the Grevy's zebra population in northern Kenya (Figs. 4.2 and 4.3). These are either protected areas, or private land where Grevy's zebra are tolerated, or even encouraged. In these areas Grevy's zebra are found significantly closer to water than in other areas (Fig. 4.2), and there are significantly higher percentages of lactating females (Fig. 4.3). This emphasises the inverse relationship between the mean distance from water that Grevy's zebra populations are found, and recruitment.

4.4.0.2 Social behaviour

The results successfully discriminate between the predictions offered in the introduction (section 4.1). In areas with high livestock densities Grevy's zebra are found significantly further from water (section 4.3.0.3). The further that Grevy's zebra are found from water, the smaller are the overall ranges that the population is found within (Fig. 4.4) – irrespective of population size. Increased distance from water also results in the populations being significantly less randomly aggregated relative to populations that are found closer to water (Fig. 4.5), and with larger mean group sizes (Table 4.3).

The interaction term in the GLM model in Table 4.3 provides further insight into the predictions. The significant interaction indicates that when zebra are still able to use large areas but livestock density has increased and they are found further from water, they are found in smaller groups. However, when they are only found in small areas – either because these are the only resources available in the wider area, or because these are refuges from disturbance – or both, then mean group size is larger. Inspection of the data by area reveals that area 7 (see Table 4.2) is being accounted for in the first part of the interaction. In area 7 zebra were found over a large range, but at very low density. Area 7 is semi-desert to desert (see Chapter 2), and these data suggest that there is no single patch of resources available for Grevy's zebra to congregate on as in the other areas with high livestock densities. They thus roam widely in search of small patches of resources.

These findings are especially surprising given the social biology of Grevy's zebra – where associations are typically fluid and home range size large. This is especially the case amongst non-lactating females, and it has been shown that the populations of zebra living sympatrically with higher densities of livestock have much higher percentages of non-lactating females (i.e. low percentages of lactating females). Thus, the hypothesis from these findings is that in areas of high livestock density Grevy's zebra seek refuge on patches of resources available to them by virtue of their being less water-restricted than livestock and humans. In the heterogeneous and semi-arid northern Kenyan ecosystem, these resource patches are scarce, hence they are able to range less widely, they are over-dispersed, and they occur in larger group sizes in these areas.

It is likely that these observed differences in patterns of association will also affect social behaviour, and hence possibly recruitment. The fluidity of association of Grevy's zebra is argued to result from competition between females for grass, weakening bonds between females with different water needs and abilities to travel (Rubenstein & Hack, in press). Territoriality and resource defence is the male response – attempting to maximise reproductive success (Ginsberg, 1989) when competition means that stable associations with females are not in a female's best interests (Rubenstein & Hack, in press). This is borne out in areas with low livestock densities where Grevy's zebra range widely and patterns of association are more random.

However, in areas of high livestock density Grevy's zebra range less widely, have less random patterns of association, and are found in larger groups. Given the increased local densities of females within these areas, and their being more likely to be found in larger groups, and hence more tolerant of competition, it is not inconceivable that it might be in a male's best interests to defend a harem of females rather than the resources that attract them (see Klingel, 1974).

5. Concluding discussion

As set out in the introduction, my goals in this study have been to provide accurate population size estimates and distribution data on Grevy's zebra throughout northern Kenya, while investigating differences in the structure and ecology of populations which might suggest causes for what can now be accurately described as a dramatic decline in numbers. These data are fundamental for a species now listed as Endangered (IUCN, 2003), but whose previous population size estimates have been flawed, using techniques that were unable to provide distribution data or population specific estimates (see section 1.2.1). I have also explored the possible mechanisms for local declines, drawing on work which concluded that pastoralists and their livestock compete for critical resources with Grevy's zebra (Williams, 1998b).

This work has fallen within Caughley's (1994; Caughley & Gunn, 1996) declining-population paradigm in an effort to ascertain and identify the "problem" (Asquith, 2001). Any possible mechanisms identified also fit within this paradigm. However, the results have shown that a number of the populations are small and isolated; they fall within the small-population paradigm (Caughley, 1994; Caughley & Gunn, 1996).

But this is not the end, either of vital research, crucial conservation actions, or hopefully of Grevy's zebra! This study was initiated to provide essential baseline data from which a conservation program could be developed – for which the estimates are vital – allowing populations to be assessed within both of Caughley's paradigms. The practical difficulties of conducting a survey that covers all Grevy's zebra range in an extremely remote and insecure area, followed by the arduous task of processing, scanning, coding and analysing over 10000 images have been challenging

– but the result will be, I hope, of significant importance in contributing to the future conservation of Grevy's zebra.

In this final chapter I will summarise the key findings of this study and relate them to wider issues in conservation biology. Specifically I will discuss what lessons we might learn from this study and the priorities for future work, especially their implication for conservation in northern Kenya.

5.1 Key findings

1. The final estimate for Grevy's zebra in northern Kenya is 2571 (95% confidence interval 2435 - 2707) is reliable with narrow confidence limits
The majority of the population (87%) were found in the south of the current range. The survey has resulted in a further key output: the invaluable resource of a database that contains the identities of 74% of all Grevy's zebra in northern Kenya.

2. A current distribution map of populations is now available (Fig. 5.1).
The six northern populations were small and potentially isolated. Significant range contraction and intrinsic diversity loss are a real possibility.

3. High densities of livestock lead to lower recruitment in zebra populations.
In arid areas with high livestock densities, there were fewer lactating females – and those that there were, were found further from water. Thus, I suggest that this had a negative effect on recruitment within these populations.

4. Social behaviour is altered in areas of sympatry with livestock.
In arid areas with high livestock densities, where Grevy's zebra were found further from water, the zebras ranged over smaller areas and were found in over-dispersed and larger aggregations.

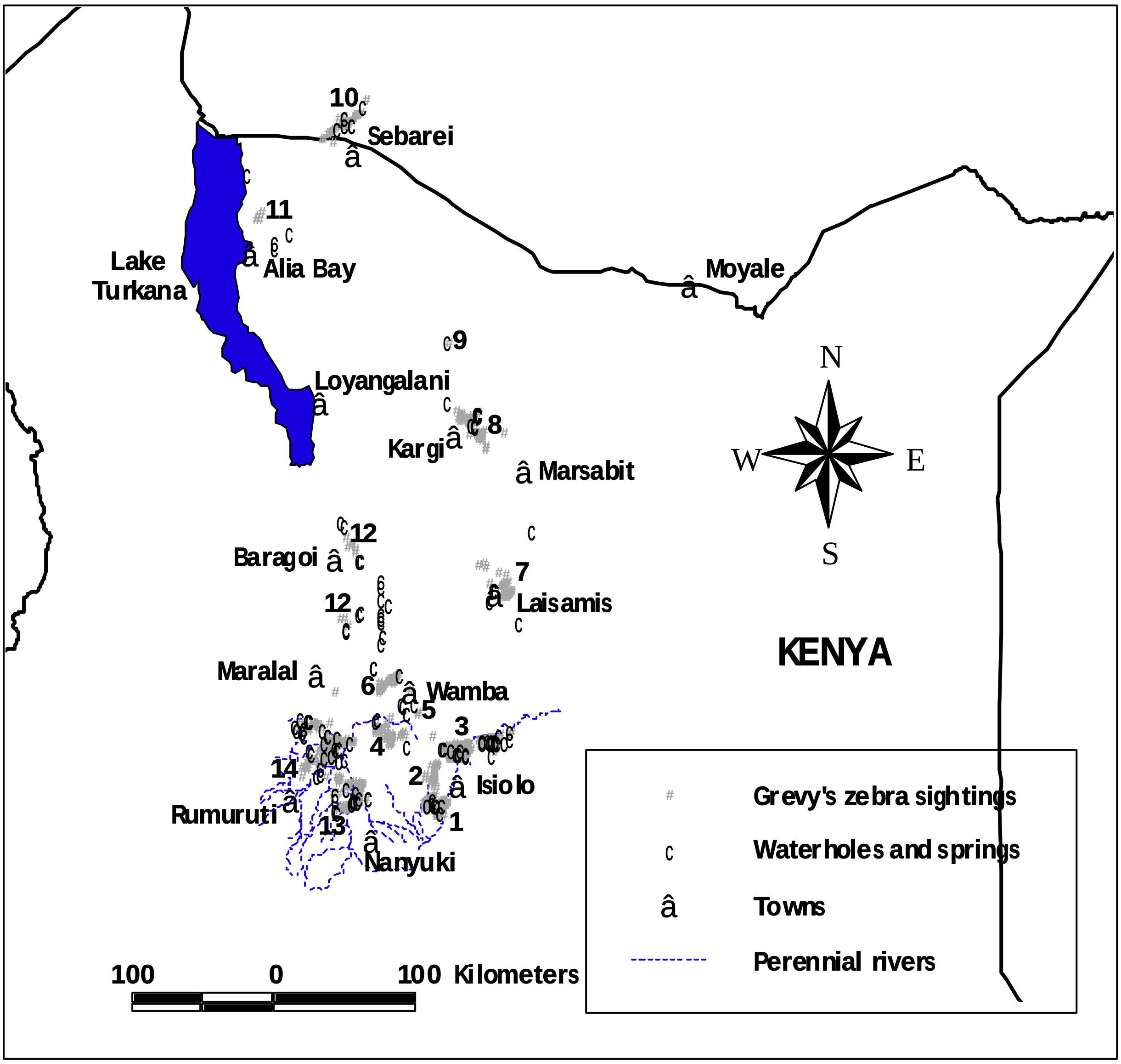

Figure 5.1: Current distribution of Grevy's zebra in northern Kenya derived from the results of this study. Numbers next to each population are the area numbers used in this survey c.f. Table 3.3 for population estimates.

5.2 Putting it in perspective...

5.2.1 Populations, pattern and process

Conservation biologists have responded to the bleak future of the current extinction threat in three main ways (Balmford *et al.*, 1998): 1) identifying the causes of the decline (declining population paradigm); 2) examining the effects of small population size itself (small population paradigm), and 3) more recently efforts with area-selection techniques (Caughley, 1994; Williams, 1998a). These approaches are all based on contemporary patterns, and neglect processes that might be occurring, particularly on larger scales (Balmford *et al.*, 1998; Smith *et al.*, 1993). At a species level these are likely to be occurring between populations, e.g. metapopulation and genetic processes. Recent work has highlighted the importance of populations to reflect short-term changes that the lag-time of species monitoring renders obsolete (Balmford *et al.*, 2003).

This study has focused on the populations – providing population abundance estimates, distribution data, and correlates of the effects of livestock density on population recruitment and aggregative behaviour. A conservation strategy for Grevy's zebra might now effect a variety of options: 1) focus only on those populations where livestock density is low, recruitment high and land-owners tolerant; 2) tackle the mechanisms of decline, e.g. by protecting the small areas where the more isolated populations occur; and/or 3) protect diversity with relocations and by emphasising captive breeding. But do any of these secure the processes that are maintaining what they set out to conserve?

Recent viability studies suggest that contiguous populations of thousands of individuals might be needed to ensure long-term persistence in the wild (Reed *et al.*, 2003). Bottlenecks leave the population less adaptable to environmental stress in the long-term, despite any short-term recovery (Reed & Bryant, 2000). Captive breeders often favour certain Grevy's zebra phenotypes, and hence reduce diversity or possibly the ability even to survive in the wild (U. Rademacher *pers. comm.*). While the constant threat of political and economic instability in developing countries should further caution against putting all of one's Grevy's zebra in one Kenyan basket.

But how realistic is it to attempt to conserve all of northern Kenya's Grevy's zebra populations, and have enough impact on the human-dominated matrix in between to maintain routes for dispersal?

5.2.2 Livestock, grazing and water

Semi-arid ecosystems can be conceptualised as existing in several alternative 'states', with transitions between states triggered by perturbations and disturbances (Canney, 2001; Packer, 1999). They have a history of climatic variability, and have undoubtedly co-evolved with a range of herbivores (Archer *et al.*, 1996). However, the implication is that heavy sustained grazing by one herbivore species may be an atypical disturbance that reduces the diversity and resilience of the system.

Ludwig *et al.* (1997) suggest that water points, when sparsely distributed, cause severe but localised degradation, but that as the density of water points increases, grazing becomes less intensive and more evenly distributed. However, de Leeuw *et al.* (2001) found that in northern Kenya when waterpoints are sparsely distributed livestock clusters around them and wildlife occupy the more remote areas in between, but that when waterpoints are in a denser network, livestock are more evenly distributed and wildlife virtually absent. This scenario would reduce the heterogeneity that might maintain resilience in semi-arid systems, and facilitate over-utilisation.

The development of water sources for livestock and people is one of the major interventions in rangelands. This study has attributed decreased recruitment in Grevy's zebra to increasing densities of livestock and the resultant increased distance that Grevy's zebra are found from water. The implication is that uncontrolled development of water sources in northern Kenya would further threaten those populations that live in sympatry with livestock, whilst contributing to the decline in heterogeneity of the overall ecosystem and possibly resulting in an irreversible loss of resilience.

5.3 Future work

One of the key results of the survey has been to confirm the degree to which the populations in the far north of Kenya are small and potentially isolated. They are persisting in fragile ‘refugia’, allowed them, perhaps temporarily, by the inability of humans to exploit evenly the entire landscape.

Dispersal

Movement between populations should be investigated – both in the southern range where the importance of three geographically unconnected areas for recruitment into the general population has been highlighted, and between the potentially isolated northern populations. This should include the challenging investigation of ‘who’ moves, and when, as well the survival and reproductive success of immigrants into a population. Recent technological advances in GPS and cellular technology are allowing spatial data to be collected with an unprecedented level of detail and on a scale that allows individual associations and movements to be recorded (D. Rubenstein, G. Hemson *pers. comm.*). These data are particularly vital for endangered species which most desperately need accurate viability analyses and management plans (Macdonald & Johnson, 2001).

Ecology of ‘refuge’ populations

A better understanding of the ecology of these populations, in conjunction with dispersal data, would help to focus conservation efforts and resources. There is the possibility that these are doomed populations not only because of the low recruitment that may be a function of the over-utilisation of resources in the wider area, but also because small, isolated populations are susceptible to processes inherent in their small size, e.g. demographic and genetic stochasticity, and edge effects (Balmford *et al.*, 1998;

Caughley, 1996; Haig, 1998). However, they might be stable viable entities that range over much wider areas when conditions allow.

Genetic linkages

Ideally dispersal data would be accompanied by genetic data substantiating the role of dispersal in gene flow between populations. Dispersing individuals may differ significantly on average from others in the population from which they come, and too which they go. Effective dispersal requires gene flow (Whitlock, 2001). However, isolation also maintains local variation. Knowledge of the background genetic variation in the populations would further our understanding of the history of these processes in Grevy's zebra populations in northern Kenya. These data would also provide a baseline reference if future genetic management was ever required.

Sociality in 'refuge' populations

The effect of disturbance on the sociality and mating system of Grevy's zebra in refuge populations should provide insights into the ecological factors that have shaped equid mating systems. The overdispersion and larger group sizes that this study found in 'disturbed' populations should allow hypotheses regarding the effect of the increased tolerance of competition by females on the mating system to be tested.

Improved monitoring techniques

While population monitoring is vital, the laborious work involved in collating the results of this study makes it an unappetising overall strategy for future monitoring. Digital cameras are a start, as would be driving an initiative to develop pattern-recognition software that could cope with the heterogeneity in images. Further, community based schemes show promise (D. Rubenstein *pers. comm.*), and possible monitoring techniques (e.g. spoor counts at waterpoints, or crude walked transect methods) should be further investigated and trialled in different areas.

5.4 The way forward

After nearly 3000 hours of work preparing image data for the estimation analyses, we now have empirically sound population estimates and distribution data that are vital to underpin a successful conservation strategy (see Pullin & Knight, 2001). This strategy should focus on conserving both the important patterns that have emerged from this study (e.g. the key areas for recruitment in Lewa Wildlife Conservancy; Buffalo Springs, Samburu and Shaba National Reserves, and the ranches on the Laikipia Plateau), and the underlying processes that are vital for the long-term persistence of Grevy's zebra in northern Kenya (e.g. securing water sources while maintaining the heterogeneity of water distribution that this semi-arid ecosystem depends on for its persistence). Paradoxically, part of what makes northern Kenya such a difficult place to work, e.g. localised insecurity caused by bandits, undoubtedly impacts negatively on the distribution of pastoralists and their livestock, helping to maintain heterogeneity in the ecosystem.

Our influence on the future of Grevy's zebra should not be isolated to a conservative conservation strategy that seeks to only preserve key areas. Rather we should embrace the very heterogeneity of the ecosystem within which they have evolved and pursue a adaptive multi-faceted approach that seeks to conserve both the processes that are vital to Grevy's zebra as a species, and the processes which are vital to the long-term persistence of the semi-arid northern Kenyan ecosystem

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