



UNIVERSITE DE POITIERS



CENTRE D'ETUDES BIOLOGIQUES DE CHIZE

THESE

Pour obtenir le grade de

**DOCTEUR DE L'UNIVERSITE DE POITIERS**

**(Faculté des Sciences Fondamentales et Appliquées)**

*Discipline : Physiologie, biologie des organismes, populations, interactions*

Présentée et soutenue publiquement le 14 novembre 2006 par

**Sophie Grange**

**The great dilemma of wild equids: living with  
grazing bovids and avoiding large predators?**

---

*Directeur de thèse:* Dr. Patrick Duncan

---

*Rapporteurs :* Pr. John M. Fryxell  
Pr. L. Morris Gosling  
Dr. Anne Loison

*Examineur :* Pr. Didier Bouchon

*Invité :* Dr. Jean-Michel Gaillard

## - Remerciements -

*Quand tu ne sais plus où tu vas, arrête-toi,  
retourne-toi, et regarde d'où tu viens.*

Proverbe Masai

*Avant d'entrer dans le monde impitoyable des chercheurs, je ne savais pas vraiment à quoi m'attendre : plus qu'un apprentissage de la recherche, cette thèse fut pour moi une véritable aventure humaine qui a duré trois ans et demi. Mais avant toute chose, rien de tout cela n'aurait pu se faire sans le soutien financier et surtout les encouragements permanents de mes parents : je vous remercie donc de tout mon cœur et vous dédie le fruit de ces années de travail.*

*Mon grand dilemme est bien différent de celui des équidés sauvages : c'est d'avoir travaillé durant ces trois ans et demi avec le Dr. Patrick Duncan, qui est quelqu'un que j'apprécie beaucoup, mais qui, comme tout grand chercheur et directeur de laboratoire, n'est malheureusement pas très disponible. Il a néanmoins montré un grand intérêt pour mon travail. Mais étant de nature solitaire, j'ai souvent appris par moi-même : c'est une excellente leçon de vie. Tous mes échecs sont donc miens, ainsi que toutes mes petites victoires... Je voudrais par la même occasion remercier Alison Duncan pour la tolérance et la patience dont elle a fait preuve lorsqu'au cours d'un repas la conversation devenait un peu plus scientifique et que Patrick partait dans de fascinantes discussions ! Mais en dehors du partage des connaissances et de cette passion pour l'Afrique, Patrick m'a ouvert des opportunités afin d'expérimenter différents aspects du métier de chercheur : enseignement, co-organisation d'un colloque international, montage d'un projet de recherche et gestion du terrain en Afrique (ce qui – soit dit en passant – est loin d'être la chose la plus aisée, surtout au Zimbabwe). Pour tout cela, je te remercie Patrick (vous noterez ici un tutoiement qui m'a coûté deux années d'efforts Mr. Duncan!). Mais je crois qu'en la circonstance, je vais m'adresser à l'ami plutôt qu'au « big boss » et te dire : « Asante sana » !*

*Il y a également Jean-Michel Gaillard... J'ai bien sûr une grande estime pour toi, et tu m'as toujours « encadrée » efficacement car, malgré ton emploi du temps de ministre, tu as toujours répondu avec une incroyable dextérité à mes problèmes d'analyses et de rédaction. Tu as aussi montré un réel intérêt pour mon travail et tes encouragements, ainsi que ton soutien, m'ont aidé à traverser les moments de doutes. Alors, un grand merci à toi Jean-Michel !*

*C'est grâce à Didier Bouchon que j'ai pu faire mes premières armes dans le milieu de l'enseignement universitaire. J'ai beaucoup apprécié l'intérêt et la curiosité que tu as porté sur mon travail bien qu'il ne s'agissait pas de cloportes ou autres petites bestioles dans ce genre... J'ai été touchée par la confiance que tu m'as accordée au cours de mes enseignements. Merci donc pour ton enthousiasme et tes encouragements !*

*Une thèse, c'est avant tout une période d'apprentissage, et les échanges de connaissances et de points de vues scientifiques ont été indispensables et surtout nécessaires à l'avancée de mon travail de recherche et de mes réflexions : merci donc à Jean-Michel Gaillard, Pierrick Blanchard, Norman Owen-Smith, Géraldine Fleurance, Jean Clobert, William Bond et Hervé Fritz.*

*Il y a eu bien d'autres rencontres avec divers scientifiques, que ce soit au cours du PICS France – Afrique du Sud ou bien lors de mes escapades africaines... Ce fut à la fois impressionnant et tellement atypique de se retrouver face à face avec John Skinner, de passer un mois à l'université de Wits avec Norman Owen-Smith, de visiter l'université de Pretoria avec Johan du Toit, de parler de science avec Herbert Prins à la terrasse d'un café hollandais, de faire un safari photo à Hluhluwe-iMfolozi avec Wayne Getz, de découvrir cette même réserve africaine à travers le regard avisé et amusé de William Bond, d'emmener Jean Clobert sur mon terrain « zèbres » à Hwange, et enfin de survoler le Serengeti dans le même avion que Craig Packer pour finir la soirée dans un restaurant indien à parler de prédation... Certaines rencontres ne sont restées que virtuelles à travers des e-mails, mais elles n'en ont pas été moins marquantes. Je pense bien sûr à tous mes co-auteurs sur l'article « Serengeti », et en particulier à Tony Sinclair, Peter*

Gogan et Heribert Hofer. J'ai beaucoup apprécié l'intérêt et la gentillesse de Hans Kfingel (le grand Mr « zèbre »), mais aussi de Hans Kruuk, Michel-Antoine Leblanc, et bien d'autres qui ne sont pas cités ici, mais qui ont néanmoins marqués agréablement et intellectuellement ma thèse !

Je n'oublie pas non plus les jeunes scientifiques un peu baroudeurs qui connaissent l'Afrique et avec lesquels j'ai eu d'intéressantes discussions et échanges d'e-mails. Tilo Burghardt, Dr Zoo alias Randal Arsenault, Chris Brooks, Casper Bonyongo... Mais aussi les merveilleux moments partagés à Hwange avec toi, Pierrick (merci pour ton humour et nos discussions scientifiques), et toi, Géraldine (merci pour ton soutien et ta confiance, ce fut un plaisir de partager cette expérience avec toi !).

Mais en dehors de la science, il y a aussi le quotidien d'une thèse... Faire sa thèse à Chizé est – je crois – une expérience unique au monde ! Il y a tellement de va et vient que cela fait de Chizé un endroit où l'on rencontre énormément de gens différents, et où se tissent aussi de véritables amitiés. Il est donc impossible de remercier tous les chizéens sans en oublier (alors que ceux qui ne sont pas cités ici ne m'en veulent pas !)... Certains ont bien sûr compté plus que d'autres... Je pense notamment à Nadège, Cécile R et Audrey S (qui ont supporté mes pétages de plombs), mais aussi à Christine, Cécile V, Olivier R, Simon V et Franck L (avec lesquels j'ai passé quelques uns des meilleurs moments à Chizé), et enfin à Audrey I et Fabrice (mes deux africains préférés). Chizé ne serait pas Chizé sans Nadine, Noël et Jacqueline : alors je vous remercie pour les fous rires, les bêtises, et votre générosité...

Enfin si il y a un « chizéen » qui doit être cité c'est Alban. Je te remercie pour avoir été toujours présent dans les bons comme dans les mauvais moments. Depuis Poitiers, il s'en est passé des choses : mais la plus importante c'est cette magnifique amitié que l'on partage aujourd'hui. Plus qu'un ami, tu es devenu mon meilleur ami. Tu sais écouter, conseiller et reconforter... Et tu n'imagines pas à quel point tu m'as aidée au cours de cette thèse. Merci !

On ne choisit pas sa famille, mais si j'avais eu à choisir ma petite sœur, je n'aurais pas trouvé mieux... Je suis si fière de tout ce que tu as accompli Carole. Merci d'être là !

Mes coups de cœur ont été parsemés de rencontres au cœur de l'Afrique... Alors merci à vous: Ronnie & Bob, Trish & Geoffrey (vous êtes une vraie famille pour moi), et aussi à tous les « Hwangéens » que je connais, en particulier : Owen & Ntombi, Jane, Freedom, Skippy...

J'ai également découvert le monde des médias à travers mes yeux d'apprentie scientifique. Un grand merci à Télé Images Nature pour votre « sponsoring » financier qui m'a permis de terminer cette thèse envers et contre tous ! Sans cela, il n'y aurait pas de thèse ! Ce film fut riche en expériences et en rencontres... Merci à vous : Marie, Véro, Jean-Luc, Eric... ainsi qu'aux « gars » tanzaniens et kenyans : John, Tasha, Kfialid, Moses, Hanoa...

Enfin une petite pensée pour tous ceux qui m'ont inspiré et m'inspirent toujours : mes idoles, toutes ces personnes rencontrées au hasard du chemin... , mais aussi et surtout : l'Afrique ! J'ai été contaminée par le virus africain dès l'adolescence. Pourquoi ? Comment ? Nul ne peut le dire. Ma passion pour l'Afrique, sa faune sauvage, ses habitants, ainsi que cet art et ce goût de vivre si différents, restent inexplicables ! La révélation eut lieu en l'an 2000 au milieu de Masai Mara, et depuis le rêve continue, plus réel que jamais... Je sens d'ailleurs au fond de moi qu'il ne s'arrêtera pas, une partie de mon cœur est là-bas sous ce soleil éclatant, au milieu de la savane, en harmonie avec les couleurs, les odeurs et les êtres. J'ai un besoin vital de cette terre de contrastes, parfois si dure, mais en même temps si fascinante. Jamais je ne me lasserai du port altier d'un guépard face au soleil couchant, du regard amusé ou interrogateur de mes chers zèbres, et de toute cette vie qui résonne si fort en moi quand je suis là-bas...

**PS : Un remerciement très spécial pour ceux qui m'ont aidé à franchir la dernière ligne...**

*Je souhaite sincèrement remercier ceux qui m'ont aidé à me relever et m'ont soutenu durant les toutes dernières épreuves de cette thèse. C'est surtout dans les moments difficiles que l'on reconnaît ces vrais amis...*

*Alors encore merci à vous, Papa et Maman, d'avoir été là...*

*A toi, Carole, et à ce petit bout de bonheur qui sera bientôt parmi nous...*

*A toi, Jean-Michel, pour avoir réagi aussi vite et aussi efficacement...*

*A toi, Vincent, pour cette rage qui te pousse à défendre les étudiants et à combattre l'injustice...*

*A toi, Didier, pour avoir joué si bien l'intermédiaire auprès des instances universitaires et pour ton soutien...*

*A Charly et Pablo, ainsi qu'au personnel du CEBC et aux étudiants, pour toutes leurs démonstrations de soutien...*

*A David Carslake qui a gentiment accepté de corriger l'anglais et qui a « britishly improved » mon manuscrit de thèse... Alors très sincèrement merci David !*

*Et puis plus particulièrement à mes amis qui sont là contre vents et marées... Tous ceux qui ont suivi mon histoire par e-mails : Alban, Cécile V. & Fabrice, Audrey I., Franck, Christine, Olivier R., Aurélie G., Pierrick et Christophe. Même à distance vous avez su m'apporter le soutien dont j'avais besoin !*

*Un énorme merci à ceux qui ont souvent « ramassé les morceaux et essuyé les larmes » pour que je puisse repartir de plus belle : à Nadine, Noël, Jacqueline, mais aussi Cécile R. et Audrey S. pour tout simplement avoir été là dans les moments de désespoir !*

*Enfin un grand merci à Géraldine et Nadège pour m'avoir offert non seulement un soutien sans faille, mais aussi des petits « refuges » quand tout allait de travers...*

*Et puis encore une fois... à l'Afrique ! Ma thèse fut – comme je l'ai dit – avant tout une aventure humaine, traversée par ces « trop pleins » d'émotions et de sensations qui font si intimement partis de mon caractère et de ma vie... Et c'est pour cela que j'ai vécu cette période de mon existence avec autant de passion, de forces et de faiblesses... Puissent nos rêves vivre toujours...*

*A mon Père,  
Pour m'avoir transmis son amour pour les animaux  
Et tout ce qui fait que je lui ressemble tant...*

*A ma Mère,  
Pour tout ce trop-plein d'amour qui fait sa force  
Et au travers duquel je puise la mienne...*

**Contents**

**Introduction** ..... - 4 -  
 Structure of the thesis ..... - 13 -

**Chapter 1:**

**What limits the Serengeti zebra population?** ..... - 15 -  
 Abstract ..... - 16 -  
 I - Introduction ..... - 17 -  
 II - Materials and Methods ..... - 19 -  
     1 - Study area ..... - 19 -  
     2 - Aerial and ground censuses of ungulate populations ..... - 20 -  
     3 - Vital rates ..... - 20 -  
         3.1 - Buffalo ..... - 21 -  
         3.2 - Wildebeest ..... - 21 -  
         3.3 - Zebra ..... - 21 -  
     4 - Modelling ..... - 24 -  
         4.1 - Population models ..... - 24 -  
         4.2 - Simulations ..... - 24 -  
     5 - The impact of lion and hyena predation on wildebeest, zebra and buffalo in the Serengeti ecosystem ..... - 25 -  
 III - Results ..... - 26 -  
     1 - Temporal variation in zebra age structure ..... - 26 -  
     2 - Vital rates and population models ..... - 27 -  
     3 - Elasticity analysis and generation time ..... - 27 -  
     4 - Simulating the effect of changing vital rates among species ..... - 28 -  
     5 - Estimating the annual off-take of wildebeest, zebra and buffalo by lions and hyenas ..... - 30 -  
 IV - Discussion ..... - 30 -  
     1 - Demographic processes ..... - 31 -  
     2 - Ecological processes ..... - 32 -  
 Acknowledgements ..... - 34 -  
 Appendix 1.1 ..... - 36 -  
 Comments on Chapter 1 ..... - 37 -

**Chapter 2:**

**Bottom-up and top-down processes in African ungulate communities: resources and predation acting on the relative abundance of zebra and grazing bovids** ..... - 39 -  
 Abstract ..... - 40 -  
 I - Introduction ..... - 41 -  
 II - Material and methods ..... - 42 -  
     1 - Protected areas ..... - 42 -  
     2 - Animal data ..... - 43 -  
     3 - Statistical analyses ..... - 44 -  
         3.1 - The effect of rainfall and soil quality on ungulate biomasses ..... - 45 -  
         3.2 - Predation ..... - 45 -  
 III - Results ..... - 46 -  
     1 - Rainfall and soil quality ..... - 46 -

2 - Predation .....	- 47 -
IV - Discussion.....	- 49 -
Acknowledgements .....	- 53 -
Appendix 2.1: The database on 23 African protected areas: IUCN category, area size (km <sup>2</sup> ), mean annual rainfall (1980-99), soil nutrient availability and the biomasses of medium-sized ungulates and their predators (kg/km <sup>2</sup> ). .....	- 55 -
Appendix 2.2: Species body weights .....	- 56 -

### Chapter 3:

#### **Searching among zebras...The social behaviour and population dynamics of plains**

<b>zebras: preliminary results from Hwange National Park, Zimbabwe .....</b>	<b>- 57 -</b>
Abstract .....	- 58 -
I - Introduction .....	- 59 -
II - Material and Methods.....	- 61 -
1 - Study area.....	- 61 -
2 - Identification and monitoring .....	- 62 -
3 - Statistical analysis .....	- 64 -
III – Preliminary results.....	- 65 -
1 – Changes within family groups.....	- 65 -
2 - Reproduction.....	- 67 -
3 - Survival rates .....	- 67 -
4 - Modelling.....	- 69 -
IV - Discussion.....	- 70 -
Acknowledgements .....	- 76 -
Appendix 3.1 – Goodness of fit tests with U-CARE .....	- 77 -
Appendix 3.2 – Changes within family groups between this study (12 families followed during one year) and Klingel’s study (11 families followed during one year). .....	- 77 -

### Chapter 4:

#### **Is the feralization of domestic horses a sexist process?**

<b>Abstract .....</b>	<b>- 79 -</b>
I - Introduction .....	- 80 -
II - Material and Methods.....	- 81 -
1 - Camargue horses.....	- 81 -
1.1 - The population and the study area .....	- 81 -
1.2 - Data on the horse population .....	- 82 -
2 - Analysis and modelling.....	- 83 -
2.1 - Changes in survival rates and fecundities.....	- 83 -
2.2 - Population modelling .....	- 83 -
III - Results.....	- 84 -
1 - The causes of changes in vital rates.....	- 84 -
1.1 - Horse condition, density and food resources .....	- 84 -
1.2 - Demographic parameters and other factors .....	- 85 -
1.3 - Changes between 1975-79 and 1980-83 .....	- 86 -
2 - Model simulations.....	- 87 -
3 - The pattern of changes in vital rates .....	- 88 -
IV - Discussion.....	- 89 -
Acknowledgements .....	- 95 -

<b>Discussion</b> .....	- 96 -
Synthesis.....	- 97 -
Conclusions and perspectives.....	- 103 -
<b>References</b> .....	- 106 -

## **Introduction**



*Ce que je vais vous dire n'est pas facile à entendre,  
Impossible à admettre,  
Mais si vous voulez bien écouter mon histoire,  
Si vous voulez bien me faire confiance,  
Alors peut-être que vous finirez par me croire  
Et c'est très important car vous êtes, sans le savoir,  
La seule personne au monde avec qui je puisse partager ce secret.*

Marc Lévy

During recent decades, the consequences of an increasing human pressure on animal communities and their environment have been a central issue in scientific and political debates. One major challenge for many biologists today is the preservation of natural ecosystems, with scientific work focused on the conservation and management of wildlife. It is clearly not possible to identify which ecological processes influence the functioning of ecosystems without taking into account the core component of mammal communities: the large herbivores, which stand between plants and predators (Begon *et al.* 1986, Olf *et al.* 1999). A good knowledge of their ecology is therefore essential to understand the structure and the dynamics of ecosystems. As relationships between plants, herbivores and predators shape mammal communities, the causes and consequences of variations in the relative abundances of coexisting animal species, both in space and time, are important keys to understand the functioning of ecosystems (Rosenzweig 1996). Among the various fields in ecology, the study of population dynamics provides most of the scientific basis and responses in the preservation of mammal communities and their ecosystems.

Research on population dynamics can result from two major approaches, according to the objectives and the context of the study. The first is more theoretical and concerns the development of statistical tools through model simulations to test, complete or elaborate ecological theories, principally on the variations in animal abundance. The second has many applications in terms of management and conservation and is focused on the development of population models based on empirical data. In the second case, the objective is to explain observed variations in population size. In such a context, population models generally provide information on demographic parameters for one population under given environmental conditions, and are used to study in detail the population demography, identify the critical parameters in population dynamics, and predict the future population trends.

Early studies on population dynamics were focused on the statistical estimation of the population growth rate (Malthus 1798, Verhulst 1838). Major mathematical models were subsequently developed to estimate the importance of inter- and intra-specific competition in relation to the competitive exclusion principle and the theory of limiting similarity (Mac Arthur & Levins 1967, May 1975). These statistical models consider several animal populations, and represent the basis of other scientific work based on the dynamics of predator-prey systems (Lotka 1925, Volterra 1926). Major scientific questions, like species coexistence, rely on the development of such models (Caswell 1978, Tokeshi 1999).

Theoretical concepts are necessary to establish general thoughts on ecological processes acting on animal communities, and their applications and tests in the field are essential for scientific knowledge in ecology. Indeed, to slow down the observed decline of many mammal populations in response to human activities, it is essential to determine the causes of variations in abundance within mammal communities, and consequently to study the dynamics of animal populations. For that reason, population models have been widely used in the field through demographic studies (Caughley 1977). Such studies can be done at different scales, in terms of time and space, which involve diverse approaches. Many data are available on population trends through regular or irregular game counts, and provide precious information on the current status and on population trends (*via* growth rates) of mammal species within ecosystems and across time. However, to understand which mechanisms or factors induce variations in animal abundance, data on population sizes are insufficient and a direct analysis of life history parameters is necessary. The development of matrix population models (Leslie 1966) based on age-specific vital rates (survival and fecundity) has proved to be very useful in wildlife management and ecological issues (Caswell 2001). In large mammal populations, survival rates have usually been estimated from life tables (*via* the determination of the ages of skulls collected in the field after natural deaths or harvesting operations). Fecundity rates are generally assessed *via* the examination of reproductive tracts through game cropping or animal captures. These two types of demographic rates are then integrated in matrix population models to describe or predict population trends and identify critical demographic parameters. However, the estimates of survival obtained from life table methods are often biased as they are based on the assumption of stable age structure, which is rarely encountered in mammal populations. More recently, the development of individually based studies using capture-mark-recapture (CMR) methods has provided accurate estimates of age- and sex-specific survival rates (Cormack 1964, Jolly 1965, 1982, Seber 1982). The CMR method is based on the principles of analysis of variance and linear models for survival and capture estimates and the maximum likelihood ratio for model selection (Lebreton *et al.* 1992).

Because animal populations cannot have an indefinite rate of increase, the concepts of “regulation” and “limitation” have emerged. Animal population size varies in time: it increases thanks to births and immigration, and decreases because of individual losses due to mortality and emigration. When gains and losses are balanced across time, the population size reaches its equilibrium and is relatively stable. The process determining the size of this

equilibrium is called “limitation” (Sinclair 1989, Sinclair *et al.* 2006). A limiting factor is therefore defined as a factor affecting mortality and/or birth rates, and can be density-dependent or not (*e.g.* a population can be limited by the reduction of its habitat). However, populations are always disturbed from their equilibrium size and often show fluctuations. The return to their equilibrium size *via* the effects of density-dependent factors on mortality and/or birth rates corresponds to a process called “regulation” (Sinclair 1989, Sinclair *et al.* 2006). Biotic processes, such as intra-specific competition for resources or predation, can therefore potentially lead to the regulation of large herbivore populations.

Studies on the population dynamics of mammals principally aim to explain variations in animal abundance, which is central to the identification of the regulating / limiting factors acting on these populations. This is why population modelling has become such an important tool in terms of the management and conservation of mammal species, with applications at different levels (individual, population, community). To understand the mechanisms of regulation or limitation in mammal populations, both bottom-up and top-down processes have to be considered (Sinclair 1989, Sinclair & Krebs 2002). For large herbivores, bottom-up processes concern the effects of quantitative and qualitative variations in food resources (*i.e.* plants) on the population dynamics taking into account environmental variables (rainfall, temperature, etc.), and variations in food availability due to biological components (inter- and intra-specific competition). The top-down processes include all natural enemies that could have a negative effect on the demography of the “prey” population: herbivores can be affected by predators, but also by diseases. To understand which factors limit or regulate a large herbivore population, it is necessary to take into account interactions between these three components of the mammal communities: vegetation, competing herbivore species, and natural enemies (predators and diseases). A good understanding of these interactions should allow the assessment of limiting or regulating factors acting on mammal populations, and is an essential stage in conservation projects and wildlife management.

Among medium-sized mammals, the equid family stands out in the crowd of herbivore species. Equids belong to the order Perissodactyla, which includes three families (Rhinocerotidae, Equidae and Tapiridae). During the Eocene and Oligocene, the Equidae constituted a very diverse group, including 350 species. Today only 8 species remain in the wild (Fig. 1), with five of them in Africa (Groves & Bell 2004). They comprise four zebras

(*Equus grevyi*, *Equus zebra*, *Equus hartmannae* and *Equus quagga*), one African wild ass (*Equus africanus*), two Asiatic wild asses (*Equus hemionus* and *Equus kiang*), and one wild horse (*Equus ferus przewalskii*). Studies on the population dynamics of wild equids present not only a biological interest in terms of scientific knowledge, but they are also important in ecology due to the central role of such medium-sized herbivores in ecosystems. There is also an interesting evolutionary perspective related to the coevolution and coexistence in most ecosystems of wild equids and grazing bovids. The latter are now the dominant herbivores within animal communities (Cumming 1982). After about 20 million years of coevolution there is a strong overlap between the current distributions of Equidae and Bovidae, which means that different mechanisms allow the coexistence between these herbivore species. Although similar in terms of ecology, these two families also present different adaptations. The major one concerns their digestive systems: the Equidae are hindgut fermenters and the Bovidae are ruminants (Janis 1976, Hoffmann 1989). Equids also have two rows of incisors and different social systems compared to bovids. These differences should lead equid and bovid species to adopt diverse strategies in terms of foraging and reproduction, implying differences in population dynamics.

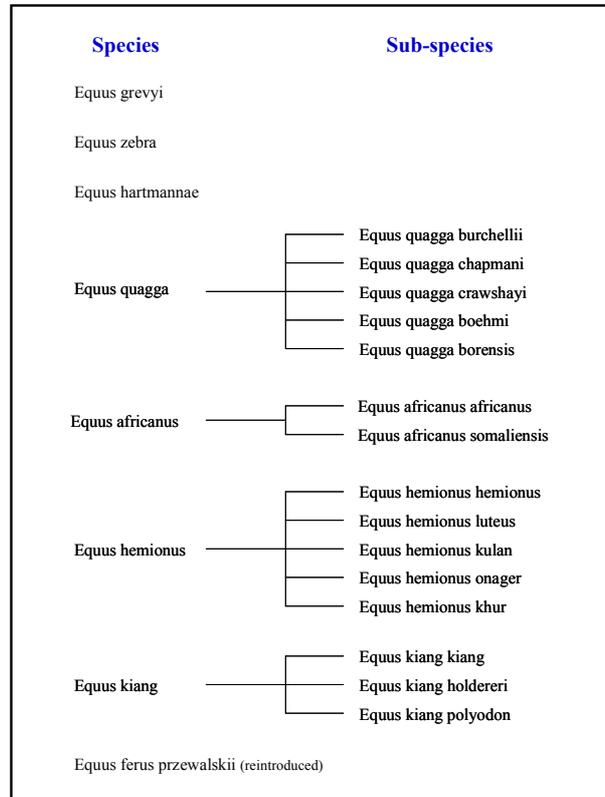


Figure 1. Taxonomy of wild Equidae (from Groves 1974 and Groves & Bell 2004)

With a high diversity of animal species and nearly natural ecosystems, Africa offers many sites ideally suited for the study of the natural processes underlying the population dynamics of large mammals. This continent still shelters 75 different species of bovids (Estes 1991) and 5 species of equids. Among wild species, plains zebra (*Equus quagga*) is the most widespread and abundant equid (Duncan 1992a, Moelhman 2002), with a current range covering Eastern and Southern African countries, from the Southern Sudan in the north to Namibia at west and South Africa in the south (Fig. 2). However during the last decade, some plains zebra populations have been extirpated from several parts of their range, principally because of overhunting and competition with livestock. Recent analyses of the taxonomy of zebras indicated that there were actually 6 subspecies of plains zebra (Groves & Bell 2004) from the northern to the southern limits of its distribution: *Equus quagga borensis*, *Equus quagga boehmi*, *Equus quagga crawshayi*, *Equus quagga chapmani*, *Equus quagga burchellii*, and *Equus quagga quagga* (now extinct). These different subspecies are characterized by variations in their stripe pattern that tends to include more brownish stripes in the southern part of their range. Plains zebras are almost exclusively grazers, and are therefore mainly associated with open habitats like grasslands and savannah woodlands. As other water-dependent species, they generally stay close to water sources (Bell 1971, Estes 1991, Skinner & Smithers 1990). In most African parks plains zebras coexist with grazing bovids of similar body size (blue wildebeest *Connochaetes taurinus* and / or African buffalo *Syncerus caffer*). As equids, plains zebras are hindgut-fermenters and use a different strategy to extract energy from their food resources compared to ruminants. Moreover the social system of plains zebras is similar to that of other wild equids (Klingel 1974, Rubenstein 1986): they live in harems, and such a social structure is likely to influence their demography. Comparative studies between plains zebras and grazing bovids, like wildebeest and buffalo, are therefore interesting in terms of ecological and demographic strategies, but there are above all essential to understand the mechanisms which led to their coexistence within African ungulate communities. Apart from competitors for food resources, plains zebras also share their habitat with large predators. Medium-sized herbivores are generally the main prey species of lion, *Panthera leo*, and spotted hyena, *Crocuta crocuta* (Schaller 1972, Kruuk 1972).

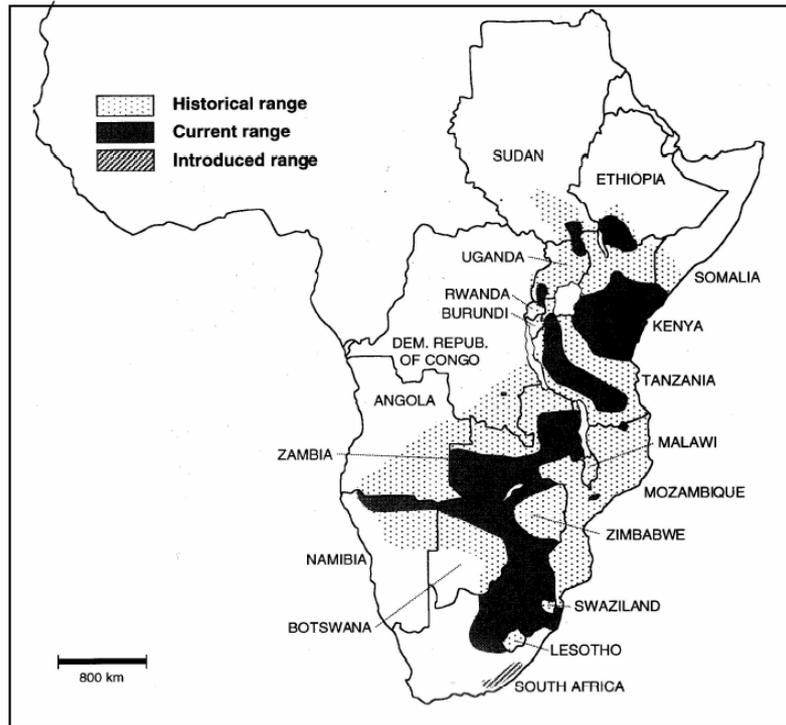


Figure 2. The historical and current ranges of the plains zebra (from Hack *et al.* 2002)

The ecology of plains zebra is relatively well-known through many studies that have investigated their spatial distribution according to their patterns of resource use (Gwynne & Bell 1968, Maddock 1979, Pienaar 1963, Brooks 2005). In the Serengeti, one of the last African ecosystems where large herbivore migrations still occur – the others are Makgadikgadi in Botswana (Brooks 2005) and Sudd Region in Sudan (Fryxell & Sinclair 1988) – Vesey-Fitzgerald (1960) showed the major role of plains zebra within the succession of herbivore species along the migration: in grazing tall grasses, zebra facilitates the use of the herb layer by wildebeest and Thomson’s gazelle. According to this, zebra populations, through their vegetation use, should have an indirect positive effect on the two other herbivore populations. Bell (1971) and Sinclair & Norton-Griffiths (1982) also confirmed this process of facilitation, but its impact on the population dynamics of these herbivores is not known. Inter-specific competition can also have an important impact on the population dynamics of coexisting ungulates. Studies of the feeding behaviour of zebra and wildebeest have shown that these two species are ecologically very similar (Ben-Sahar & Coe 1992) but have different time budgets constrained by their digestive systems (Twine 2002) leading to different impacts on vegetation. However these previous studies did not examine the effects of bottom-up factors on the comparative dynamics of these herbivore populations. Grazing bovids are generally more abundant than zebras in most African ecosystems (Cumming

1982), but the reason why is not clear. Their populations should be regulated or limited by different factors, which can lead to different population dynamics. Several studies have aimed to understand the role of climatic and geologic variables on large herbivore abundance: they have generally been done at the community level (Coe *et al.* 1976, East 1984, Fritz & Duncan 1994) or at the population level focused on only one species (Sinclair 1977, Prins 1996, Mduma *et al.* 1999). However, comparative studies on population dynamics between coexisting herbivore species are essential to understand the limiting or regulating factors acting on these populations. More recently Owen-Smith & Mason (2005), through a study on the comparative population dynamics of Kruger ungulates, showed that these populations exhibited different demographic patterns in relation to the importance of variations in their vital rates within age classes. Studies of African large predators, such as lion and spotted hyena, have mainly focused on their impact – in terms of hunting strategies and offtake – on their prey species (Schaller 1972, Kruuk 1972, Packer *et al.* 1990, Packer *et al.* 2005, Hofer & East 1993, 1995), but have never compared the relative impact of predators on the population dynamics of their different main prey species (*e.g. via* the proportion of prey mortality in different age classes attributable to predation). This is important if we want to consider the regulation or limitation of populations when several prey species coexist and are killed by the same predators. Other recent studies examined the importance of bottom-up and top-down factors on several ungulate populations in Kruger National Park (Owen-Smith *et al.* 2005, Ogutu & Owen-Smith 2005). Studies of plains zebras have been principally focused on their social behaviour (Klingel 1967, 1969a) and reproduction (Klingel 1969b, Smuts 1976a). The population dynamics of Kruger plains zebra has been studied in detail (Smuts 1976b), but there is still a real lack of accurate demographic parameters for this equid species, particularly for juveniles. Although the social system and reproductive strategies of plains zebras have been extensively investigated, nothing is really known about the regulating or limiting factors acting on their populations (Hack *et al.* 2002), or about the importance of their particular social system and reproductive strategies for their population dynamics.

In contrast, the population dynamics of feral horses has been well investigated (Welsh 1975, Berger 1986, Garrott & Taylor 1990, Garrott *et al.* 1991, Cameron *et al.* 2001). Feral horses present the same social system as plains zebras and are also confronted with predators (mainly wolves) in some parts of their home ranges. These equid populations, which have returned to the wild, now cause many problems for wildlife management, particularly in

North America where they are considered pests (Bastian *et al.* 1999, Rikoon 2006). Many research programs have therefore collected demographic data with the aim of limiting these populations: the control of reproduction has already proved to be relatively efficient in terms of horse population management (Gross 2000, Bartholow 2004). However, little information is available on the consequences of feralization (*i.e.* when domestic animals return to the wild) for the population dynamics of large herbivores. Several studies have examined the social and mating system of such populations (Hall & Hall 1988, Berteaux & Micol 1992), but none have investigated changes in population vital rates during the feralization process. As domestic large herbivores have the potential to be used in the restoration of natural ecosystems, particularly in Europe (Kampf 2000), it is essential to understand the consequences of feralization on their population dynamics to be able to manage them. For this reason, populations of large herbivores that have been monitored, but remained free from human management over long periods are of particular interest. There are two sites in Europe where such experiments have been conducted. The first is in the Oosvaardersplassen reserve in the Netherlands, where Konik horses, Heck cattle and Red deer were released in the 1980's and are unmanaged (Vulink 2001). The second is in the Camargue in Southern France, where a herd of 14 domestic horses was released in 1974 (Duncan 1992b). Their population remained unmanaged and monitored for 9 years and this study provided unique data to study the effects of feralization on the population dynamics of horses.

This thesis is focused on the population dynamics of wild equids according to their central place in ecosystems. To understand which regulating and / or limiting factors most influence wild equid populations it is important to study "natural" populations. Because of their wide distribution across African ecosystems and their coexistence with grazing bovids and large predators, plains zebras are ideal animals for studies of population dynamics. There is paradoxically relatively little information on the limitation / regulation of their populations. The first objective of this thesis is therefore to improve the knowledge on plains zebra population dynamics from previous studies, available data, and current fieldwork. In the restoration of natural ecosystems, domestic horses could be used as surrogates to replace extinct wild herbivores (Kampf 2000, Gordon *et al.* 1990), and the last part of this thesis therefore aims to identify the consequences of feralization on the demographic parameters of a Camargue horse population returning to the wild.

## **Structure of the thesis**

The first three chapters concern studies of the plains zebra, and particularly their demography in relation to their coexistence with grazing bovids and the impact of predation. The last chapter deals with the problem of reintroduction of domestic equids to the wild.

Chapter 1 presents a study on the comparative population dynamics of zebra, wildebeest and buffalo in the Serengeti, Tanzania. Many ecological studies have taken place in this well-known ecosystem and data on the demography of several ungulate species and also on large predators are available since the 1970s. Using published and unpublished data on zebra, wildebeest, buffalo and their predators, I try to answer the following question: why does the Serengeti zebra population remain so stable? I use a comparative modelling approach to identify the demographic process causing the stability of the zebra population. The ecological process is a much more difficult task and information on the ecology of these ungulates and their predators is useful to go further in the discussion about the underlying mechanism.

In chapter 2, I present an analysis of the relative importance of bottom-up and top-down processes on equids and grazing bovids coexisting in African ecosystems. This study tries to highlight some general patterns that could explain the relative abundances of these ecologically similar ungulate species. Most studies on the demography of African large herbivores have shown the importance of food resources (both in terms of quantity and quality), but the impact of predation on the prey population dynamics has been less investigated, except for few ungulate populations that experienced drastic declines (like the roan antelope population in Kruger National Park). However because of their central place in ecosystems, the populations of large herbivores are influenced both by their resources (bottom-up process) and their predators (top-down process), but the relative importance of the two processes on coexisting ungulate populations is not known. This study therefore aims to understand if bottom-up and top-down processes act in a similar way on zebra and grazing bovids, like wildebeest and buffalo.

In chapter 3, I present preliminary results on the social behaviour and demography of plains zebras in Hwange National Park, Zimbabwe. Capture-mark-recapture (CMR) methods are increasingly used for population modelling because they are the best way to obtain

accurate estimates of survival rates. As shown in chapter 1, there is a real lack of data on accurate vital rates for African ungulates, particularly for plains zebras. This demographic study based on CMR methods is the first one applied on plains zebra in Africa. The study period is too short to give precise estimates, but observations on social behaviour allow interesting comparisons with previous studies.

Chapter 4 clearly shows that the restoration of natural systems is not an easy task! The last wild horse (*Equus ferus przewalskii*) went extinct in the wild during the 1970s (Ryder 1990), and its reintroduction has been possible thanks to captive specimens kept in zoos. The main difficulties when captive animals return to the wild are to choose good individuals and to find suitable environments that will allow them to reproduce and maintain their population in the long term (Seddon & Soorae 1999). Reintroduction is not a natural process, which could lead to management problems due to non-natural behaviour and population dynamics. In Europe the restoration of natural ecosystems is based on the introduction of domestic species that are considered as surrogates of extinct wild species (Kampf 2000). When domestic animals return to the wild, they experience a process called “feralization” (or “de-domestication”), and nothing is known about its effects on the population vital rates. From a unique experiment in the Camargue, I test the effects of feralization on the demography of domestic horses. Several individuals were first released in 1974 and the population was monitored until 1984 (Duncan 1992b). The return to nature of these Camargue horses resulted in a rapid increase of animal numbers, which should have led to density-dependent effects on their demographic parameters.

## **Chapter 1:**

### **What limits the Serengeti zebra population?**

Sophie Grange, Patrick Duncan, Jean-Michel Gaillard, Anthony R. E. Sinclair, Peter J. P. Gogan, Craig Packer, Heribert Hofer and Marion East

Oecologia (2004), 140: 523-532



## **Abstract**

The populations of the ecologically dominant ungulates in the Serengeti ecosystem (zebra, wildebeest and buffalo) have shown markedly different trends since the 1960s: the two ruminants both irrupted after the elimination of rinderpest in 1960, while the zebras have remained stable. The ruminants are resource limited (though parts of the buffalo population have been limited by poaching since the 1980s). The zebras' resource acquisition tactics should allow them to outcompete the ruminants, but their greater spatial dispersion makes them more available to predators, and it has been suggested that this population is limited by predation. To investigate the mechanisms involved in the population dynamics of Serengeti zebra, we compared population dynamics among the three species using demographic models based on age-class-specific survival and fecundity. The only major difference between zebra and the two ruminants occurred in the first-year survival. We show that wildebeest have a higher reproductive potential than zebra (younger age at first breeding and shorter generation time). Nevertheless, these differences in reproduction cannot account for the observed differences in the population trends between the zebra and the ruminants. On the other hand, among-species differences in first-year survival are great enough to account for the constancy of zebra population size. We conclude that the very low first year survival of zebra limits this population. We provide new data on predation in the Serengeti and show that, as in other ecosystems, predation rates on zebras are high, so predation could hold the population in a "predator pit". However, lion and hyena feed principally on adult zebras, and further work is required to discover the process involved in the high mortality of foals.

**Keywords:** Coexistence, African ungulates, Equids, Bovids, Population dynamics

## I - Introduction

An important aspect of community ecology is to understand the mechanisms which structure multi-species assemblages in natural ecosystems. Large mammal herbivores are of particular interest because they are commonly “keystone” species, so variations in the species composition of ungulate communities can have powerful impacts on the structure and functioning of whole ecosystems. Ungulate communities in Africa are the richest of any continent, with about 100 species, which are mostly bovids (75%), though equids coexist with them in virtually all ecosystems (Cumming 1982). A well-known example is the Serengeti ecosystem (Tanzania) which has high biodiversity and where long-term data are available on ungulate populations. The two dominant bovids are the wildebeest, *Connochaetes taurinus*, and buffalo, *Syncerus caffer*, which coexist with one equid (plains zebra, *Equus burchelli*).

In the early 1960s, the numbers of zebra and wildebeest in the Serengeti were about the same (*ca.* 200,000). These two species that have evolved in parallel have similar body size, and very similar patterns of resource use (Gwynne and Bell 1968; Maddock 1979; Hansen *et al.* 1985). These ecological similarities mean that there is a potential for interspecific competition for food resources between plains zebra and wildebeest (Bell 1970; Sinclair 1977; De Boer and Prins 1990). Before 1960 the Serengeti populations of wildebeest and buffalo were limited by rinderpest, a viral disease. After its eradication in the early 1960s these two ruminant populations grew exponentially (Sinclair 1977; Mduma *et al.* 1999) until limited by resources (or poaching) after 1980 (Dublin *et al.* 1990). The zebra population, which was unaffected by rinderpest, remained remarkably constant in size during this period (Fig. 1.1). The exponential increase in wildebeest and buffalo proves that in 1960 the community of grazers in the Serengeti was not at carrying capacity, and that they were not resource limited at that time. As the foraging tactics of equids can allow them to acquire nutrients at much higher rates than bovids, zebra should have a competitive advantage over ruminants in grassland ecosystems, so we would expect that when food became limiting in the 1980s zebra should have outnumbered the ruminants (Duncan *et al.* 1990; Ménard *et al.* 2002). In spite of this physiological advantage, the Serengeti zebras have remained at the same population level since 1960. In particular the zebra population did not decrease when the populations of these two ruminants increased sharply, reaching in 1972 a biomass 4 times higher than in 1962: interspecific competition for resources clearly did not have a major impact on the Serengeti zebra population. The differences in population trends observed after

1960 suggest that the zebra population was not influenced by the same limiting factors as wildebeest and buffalo (Sinclair and Norton-Griffiths 1982).

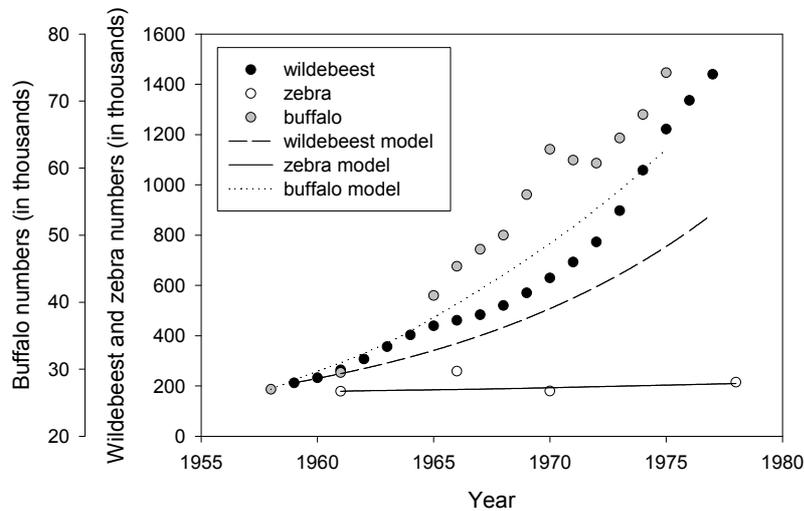


Fig 1.1. Population sizes (symbols) and model simulations (lines) of wildebeest, zebra and buffalo populations between 1958 and 1978. The population sizes are given by Mduma *et al.* (1999), Sinclair and Arcese (1995) and Sinclair (1977)

Two major processes determine the abundance of animal populations: resource competition (a “bottom-up” process) and/or predation (a “top-down” process; Hairston *et al.* 1960). In the Serengeti ecosystem long-term studies on buffalo (Sinclair 1974, 1977) and wildebeest (Sinclair *et al.* 1985) demonstrated that predation did not have a major impact on these populations which were mainly regulated by food supply, especially during dry years.

Little information is available on plains zebra demography in the Serengeti ecosystem. A comparative analysis based on the dynamics of 12 ungulate populations in the Kruger National Park (South Africa) demonstrated that zebras are less sensitive to droughts than most bovids (Ogutu and Owen-Smith 2003). Another study in the Kruger National Park demonstrated that in comparison to buffalo and wildebeest, zebra showed a weaker trade-off between nutritional requirements and surface-water constraints (Redfern *et al.* 2003). These studies suggest that zebra should be less sensitive to resource limitation compared to ruminants. In Laikipia District (Kenya), where the density of large predators is about 5 times lower than in the Serengeti ecosystem (Bauer 2003), rainfall, and consequently resource availability, strongly influences the abundance of plains zebras (Georgiadis *et al.* 2003). Conversely in Etosha National Park, periods of low rainfall have no influence on the zebra

population which seems to be mostly limited by predation (Gasaway *et al.* 1996), and where predators are abundant, zebras do suffer heavy predation, notably the young age-classes (Cooper 1990; Mills and Shenk 1992). For the Serengeti, the abundance of large predators and the behaviour of the zebras and their population trends suggest that this population may be mainly limited by predation (Sinclair 1985).

The life history tactic of a species can constrain the response of the population to environmental pressures, and thereby population trends. Perissodactyls breed later, have longer gestation periods and lower fecundity compared to Artiodactyls of similar size (Van Wieren 1996). Both the rate of recruitment and the maximum rate of increase should therefore be lower in zebra populations than in similar-sized Artiodactyls. Such a constraint may strengthen the effect of other factors, like predation, to limit zebra population sizes. We therefore expect zebra to show dampened responses to environmental variations compared with the more productive wildebeest and buffalo, because variation in population size over time is positively related to population growth rate (Sinclair 1997).

In this paper we used the long-term data from the Serengeti ecosystem to clarify the issue of the limitation of the zebra population by testing the following predictions:

1. According to the predation hypothesis, zebra should have lower survival rates than the ruminants, especially during their first year when they are most sensitive to predators.
2. Zebra should have lower fecundity and a longer generation time than these ruminants.

We built demographic models for buffalo, wildebeest and zebra, and then compared the population trends obtained from modelling with those observed from censuses. We used demographic simulations to determine which vital rates could account for the striking differences observed in population kinetics between zebra and the two ruminant species. Finally, in order to test whether the ecological mechanism involved could be predation, we estimate the offtake of zebras by predators.

## **II - Materials and Methods**

### 1 - Study area

The Serengeti ecosystem is in southern Kenya and northern Tanzania, and covers 25,000 km<sup>2</sup> (34–36°E, 1°15'–3°30'S). Rainfall shows a north-west to south-east gradient, decreasing from 1,100 to 500 mm and is seasonal with the wet season between November and June. This ecosystem is characterised by large herds of migrating ungulates, and also by high concentrations of large predators, with approximately 0.3 hyaenas/km<sup>2</sup> and 0.1 lions/km<sup>2</sup> (Sinclair and Norton-Griffiths 1979; Sinclair and Arcese 1995).

## 2 - Aerial and ground censuses of ungulate populations

Aerial and ground censuses of wildlife populations have been conducted from 1958 to 1999. Aerial censuses were performed by a pilot and one or two observers in each aircraft. Total counts were used for buffalo: each herd size was estimated from the air, and most herds were also counted on aerial photographs. The latter counts were used, except where photographs were not available. The wildebeest population censuses were based on aerial transects on each of which about 20 vertical photographs were taken at known altitude. The density of animals was calculated for each photo, and the population size calculated using Jolly's method (1969; see Mduma *et al.* 1999 for details). Population structure (sex and age class) was determined for buffalo from aerial and ground censuses, using a method based on horn shape and size (Sinclair 1977). The wildebeest and zebra population structures were obtained from ground counts (Watson 1967; Mduma *et al.* 1999; A. R. E. Sinclair, personal observation).

We restricted our analyses to the phase of exponential growth for wildebeest and buffalo populations: 1958–1978 (Fig. 1.1). To test the validity of our models, we estimated the finite rate of increase ( $\lambda$ ) from census data using the regression method for buffalo and wildebeest:  $\ln N = a + \ln \lambda \times t$  (Lebreton and Millier 1982; where  $a$  is a constant, and  $N$  represents the total population size in year  $t$ ). As there were only four zebra censuses between 1961 and 1978, we used another estimator for this population:  $\lambda = (N_t / N_0)^{1/t}$  (Lebreton and Millier 1982; where  $N_0$  represents the initial population size,  $N_t$  the population size in year  $t$ , and  $t$  is the number of years).

## 3 - Vital rates

Estimates of survival and fecundity rates for zebra and the two ruminants from the long-term studies in the Serengeti are given in Table 1.1.

### 3.1 - Buffalo

Pregnancy rates were estimated from examination of female reproductive tracts (n=69, from shot samples between 1967 and 1969); care was taken to avoid bias with respect to sex and age classes (Sinclair 1977). Survival rates of female buffalo were obtained from a life table (Sinclair 1977) constructed during the exponential stage of population increase (246 female skulls collected between 1965 and 1969). Age determination was based on the tooth-eruption pattern (Grimsdell 1973) and horn shape. Mortality rates were estimated from the life table, taking into account the exponential growth rate of the population ( $r=0.077$ ).

Table 1.1. Vital rates used in the buffalo, wildebeest, and zebra models. The data for zebra juveniles are given with 95% confidence intervals

Parameter	Age classes	Species		
		Buffalo <sup>(a)</sup>	Zebra <sup>(c, d)</sup>	Wildebeest <sup>(b)</sup>
Survival				
	First year	0.670	0.389 [0.297-0.480]	0.746
	Yearling	0.860	0.847 [0.724-0.970]	0.885
	2-year-olds	0.981	0.979	0.865
	3 to 5 year-olds	0.971	0.954	0.888
	Mature female	0.927	0.875	0.792
	Senescent female	0.599	0.768	0.780
Fecundity				
	2-year-olds	0	0	0.371
	3 to 5 year-olds	0.200	0.686	0.889
	Mature female	0.820	0.883	0.945
	Senescent female	0.660	0.883	0.945

*Data sources: (a) Sinclair (1977); (b) A. R. E. Sinclair (unpublished data); (c) R. O. Skoog and P. J. P. Gogan (unpublished data); (d) Watson (1967)*

### 3.2 - Wildebeest

Pregnancy rates were estimated from shot samples between 1964 and 1966: 153 cows from the Serengeti population were shot by National Park Wardens. Female survival and fecundity rates were obtained from a life table derived from the age distribution of female deaths over the period 1962–1965 in the Serengeti ecosystem (Watson 1967, 1969).

### 3.3 - Zebra

Zebra pregnancy rates were calculated from 178 females shot by the Tanzania Game Department in 1969–1971 (Table 1.2) and age structure of adult females during the same

period derived from ground counts and the shot sample (R. O. Skoog and P. J. P. Gogan, unpublished data). Survival estimates were also calculated from data collated for the Loliondo zebras (one of the four subpopulations in the Serengeti ecosystem; R. O. Skoog and P. J. P. Gogan, unpublished data; Table 1.3). We built a life table based on the shot sample age structure, assuming that this sample was not biased and was representative of the age distribution in the living population. The number of foals was corrected and estimated from the number of reproductive females in the sample and their fecundities, and the proportions of individuals surviving at the start of each age class ( $l_x$ ) were smoothed by a polynomial regression. The life table provided adult survival estimates (>2 year olds) for zebra females, consistent with the estimates calculated by Spinage (1972) for the Akagera zebra population. We therefore assumed that these estimates are sufficiently accurate because adult survival rates are rather resilient to environmental variation in ungulates (Gaillard *et al.* 1998, 2000a for reviews). The trends in the two populations were similar since the Akagera zebra population was near stationary in the 1960s (Spinage 1972), while the Serengeti population may have declined slightly between 1961 (n=179,000, Sinclair and Norton-Griffiths 1979) and 1996 (n=150,834, Moehlman 2002).

Table 1.2. Age structure and pregnancy rates for female zebra in the Serengeti ecosystem

Age class	Age	% of adult females (n=134)	Number of females	% pregnant	Pregnancy Rate
Subadults	3-5 yrs		33	68.6	0.686
Adults	5-8 yrs	0.51	65	81.5	
	9-12 yrs	0.36	45	93.3	
	13-16 yrs	0.08	10	90	0.883
	17-20+ yrs	0.05	7	85.7	
	not aged		18	100	

Table 1.3. Shot sample of females from the Loliondo zebra population (1969–1970)

Age class	Number of shot females (n=205)
Foals	4
yearlings	15
2 yrs	14
3 yrs	20
4yrs	18
5-8 yrs	68
9-12 yrs	48
13-16 yrs	11
17-20+ yrs	7

For Serengeti plains zebra, no individually based estimates of foal and yearling survival are available. As these vary widely both between and within ungulate populations (Gaillard *et al.* 1998, 2000a for reviews), we used data on the Serengeti zebra population structure: over 20 years a sample of the population was classified by one observer (A. R. E. Sinclair) into adults, yearlings and foals on the basis of their shoulder height, using criteria from H. Klingel (personal communication; Table 1.4). We estimated the survival rates from variations in the proportions of foals and yearlings in successive years (see Appendix 1.1) since more accurate estimates are not available, recognizing that these estimates are subject to error.

Table 1.4. Data on sex/age structure of zebra herds in the Serengeti ecosystem between 1980 and 1999; with mean annual rainfall (Annual) and dry season rainfall (Dry)

Year	Month	Season	Foals	Yearlings	Adults	Total sample	% foals	% yearlings	“Annual” (mm)	“Dry” (mm)
1980	5	wet	517	327	2846	3690	0.140	0.089	581.4	48.3
1982	5	wet	685	616	2978	4279	0.160	0.144	716.5	55.9
1983	7	wet	439	464	1933	2836	0.155	0.164	610	165
1984	8	dry	453	352	1946	2751	0.165	0.128	410	146
1986	5	wet	705	667	3025	4397	0.160	0.152	675	88
1987	9	dry	549	606	2566	3721	0.148	0.163	763	61
1987	11	dry	115	137	292	544	0.211	0.252	763	61
1988	6	wet	97	118	627	842	0.115	0.140	656	186
1989	2	wet	311	256	1835	2402	0.129	0.107	856	135
1989	7	wet	531	525	2710	3766	0.141	0.139	856	135
1990	2	wet	406	360	2662	3428	0.118	0.105	785	41
1990	6	wet	286	115	883	1284	0.223	0.090	795	41
1991	1	dry	194	114	935	1243	0.156	0.092		
1992	7	wet	83	97	495	675	0.123	0.144	815	118
1993	1	dry	187	102	918	1207	0.155	0.085	705	77
1993	6	wet	146	91	637	874	0.167	0.104	705	77
1994	1	dry	76	93	666	835	0.091	0.111	943	98
1994	4	wet	82	173	1027	1282	0.064	0.135	943	98
1994	11	dry	53	50	652	755	0.070	0.066	943	98
1997	7	wet	333	261	1469	2063	0.161	0.127	856.9	117
1998	12	dry	16	6	68	90	0.178	0.067	822	116
1999	7	wet	52	29	153	234	0.222	0.124	614	110

We tested for effects of rainfall on zebra age structure between 1980 and 1999 using logistic models to analyse variations in foal or yearling proportions in relation to season (dry vs. wet) and rainfall (annual rainfall and dry season rainfall). The rainfall data are from the Banagi station, approximately in the centre of the Serengeti National Park; the year was taken as November–October and the dry season as May–October, and data are available for all the years except 1991.

## 4 - Modelling

### *4.1 - Population models*

We used pre-breeding models based on Leslie matrices (Caswell 2001). Each population was divided into six age-classes: calf or foal (the first year of life), yearlings (1–2 year olds), 2 year olds (2–3 year olds), 3–5 year olds, mature females (5–11 year olds for buffalo, and 5–13 year olds for zebra and wildebeest), and senescent females (>11 year olds for buffalo, and >13 year olds for zebra and wildebeest; Table 1.1).

The models are based on females, assuming that male numbers are not limiting. We also considered an equal sex ratio at birth (see Sinclair 1977 for buffalo; Watson 1967 for wildebeest). For the three species, fecundity was assumed to be equal to the pregnancy rate. This assumes that very little resorption or abortion occurred: the incidence of Brucellosis is low in Serengeti ruminants and absent in zebras (Sinclair 1977).

Simulations were performed using the ULM software (Legendre and Clobert 1995). For each population, an elasticity analysis was performed on the survival rates of first-year animals, yearlings and adults, and on female fecundity (>3 year olds for buffalo and zebra, >2 year olds for wildebeest). For each simulation, outputs are the estimated population size (in successive years) and the  $\lambda$ . We also used ULM to estimate demographic outputs such as the natural rate of increase ( $r$ ) and the generation time (sensu Leslie 1966), denoted as  $\bar{T}$ .

### *4.2 - Simulations*

We used the models to simulate the effects of variations in the first year survival. According to the predation hypothesis, we predicted that:

1. Replacing foal survival in the zebra model with estimates of calf survival for wildebeest or buffalo should lead the zebra population to increase strongly.
2. Replacing calf survival in the wildebeest or buffalo models with estimates of zebra foal survival should lead the wildebeest and buffalo populations to stop growing.

We then tested the demographic impact of switching reproductive parameters among species. Since zebra fecundity should be lower and generation time longer, we predicted that:

1. Replacing the reproductive rates of buffalo and wildebeest with the zebra values should lead the wildebeest and buffalo populations to stop growing.
2. Replacing reproductive rates of zebra with the buffalo and wildebeest values should lead the zebra population to increase.

5 - The impact of lion and hyena predation on wildebeest, zebra and buffalo in the Serengeti ecosystem

Lions and hyenas account for about 85% of the predation on large herbivores in the Serengeti (Schaller 1972), so we focus our analysis on these two species. The functional and numerical responses of the predators to the increase in the ruminant populations cannot be described in detail, but data are available on changes in the diet and numbers of lions and hyenas between the late 1960s (referred as pre-1970) and the period of peak numbers of the ruminants (post-1975). The impact of predation is measured as the annual offtake of each prey species (numbers of herbivores killed by lions and hyenas) and can be expressed as a percentage of the prey population size.

An estimate of the offtake of wildebeest, zebra and buffalo by lions in the pre-1970 period is provided by Schaller (1972), based on an estimate of the amount of prey consumed per lion per day (kg), the number of lions, their diet (percentage of kills) and the average body mass of the different prey. We estimated the offtake for the period post-1975 using the same method, taking into account the increase of about 40% in the lion population since the pre-1970 period (C. Packer, unpublished data) and the diet of the lions in the period of peak numbers of ruminants (post-1975; see Table 1.5).

Table 1.5. Changes in the numbers of different prey species in the diets of lions between the pre-1970 and the post-1975 periods (Schaller 1972; C. Packer, unpublished data)

Prey species	% in lion diet	
	Pre-1970	Post-1975
Wildebeest	20-25	41
Zebra	30	24
Buffalo	15	15

For hyena predation, we used the estimates for the pre-1970 and the post-1975 periods (H. Hofer and M. East, unpublished data) and applied the same method as Kruuk (1972) to calculate the off-take of different prey species (Table 1.6). We took into account changes in

hyena diet between our two study periods (Table 1.7) and the strong increase in hyena numbers (133% of increase between our two study periods; H. Hofer and M. East, unpublished data), which lead respectively to 3,285,000 and 7,654,050 kg of prey consumed by hyena in the pre-1970 and in the post-1975 periods.

Table 1.6. Comparison of the combined off-take of zebra, wildebeest and buffalo by lion and hyena between the pre-1970 and the post- 1975 periods (data from Schaller 1972; Kruuk 1972; Hofer and East 1995; C. Packer, unpublished data; H. Hofer and M. East, unpublished data)

	Pre-1970			Post-1975		
	Wildebeest	Zebra	Buffalo	Wildebeest	Zebra	Buffalo
Lion	14 028	10 834	2 115	35 786	12 135	2 961
Hyena	8 475	5 310	161	24 135	4 285	4 728
Total	22 503	16 144	2 276	59 921	16 420	7 689

Table 1.7. Changes in the numbers of different prey species in the diets of hyenas between the pre-1970 and the post-1975 periods (Kruuk 1972; H. Hofer and M. East, unpublished data)

Prey species	% in hyena diet	
	Pre-1970	Post-1975
Wildebeest	19.4-43.8	49
Zebra	19.4-20.0	8.7
Buffalo	0.6	9.6
Gazelle	48.6-21.9	14.5
Others	12.1-13.7	18.3

We used 200,000 for the zebra population size during the whole study period, 490,000 and 1,200,000 wildebeest and 48,000 and 74,000 buffalo, respectively in the pre-1970 and in the post-1975 periods (see Sinclair 1977; Sinclair and Arcese 1995; Mduma *et al.* 1999).

### III - Results

#### 1 - Temporal variation in zebra age structure

There was no significant effect of “season” on the proportion of foals (Table 1.8). Between 1980 and 1999, the proportion of foals was strongly and negatively influenced by the mean annual rainfall, so in wet periods the proportion of foals declined. The same pattern, but much weaker, was observed with dry season rainfall.

For yearlings there was a weak and barely significant effect of season, with higher proportions of yearlings in the wet season. In contrast to the foals, there was a strong positive relationship with the dry season rainfall (Table 1.8).

Table 1.8. Logistic models with young zebra proportions (foals and yearlings). For abbreviations, see Table 1.4

Logistic model	Factor	Estimate	Standard Error	z value	p value
Foal proportion	Season	0.04190	0.03328	1.259	0.2080
	Annual	-0.00081	0.00011	-7.445	<0.0001
	Dry	-0.00075	0.00033	-2.276	0.0229 *
Yearling proportion	Season	-7.076e <sup>-2</sup>	3.442e <sup>-2</sup>	-2.055	0.0398 *
	Annual	-1.036e <sup>-5</sup>	1.120e <sup>-4</sup>	-0.093	0.9263
	Dry	1.511e <sup>-3</sup>	3.481e <sup>-4</sup>	4.340	<0.0001

Signif. code: \* p < 0.05

## 2 - Vital rates and population models

Wildebeest females may calve at 2 years of age, 1 year before zebra and buffalo females. Adult fecundity differed little among the species, except for 3–5 years old buffalo, which had lower fecundity than the other two species. Adult zebras showed intermediate fecundity compared to the ruminants. The age-dependent survival rates were similar among species except for first-year animals (Table 1.1): the ruminants were about twice as likely to survive over their first year of life as zebra.

The estimates of  $\lambda$  obtained from modelling matched closely those calculated from censuses but for wildebeest the matrix model led to a slight underestimate of the observed rate of population increase (Table 1.9).

These simple demographic models led to patterns broadly consistent with the observed trends. The first prediction, that survival is lower in young zebras than in wildebeest and buffalo, is supported. On the other hand, we did not find support for the second prediction as the fecundity of the zebra was intermediate between the values for the two ruminants.

## 3 - Elasticity analysis and generation time

Elasticities of first-year and adult survival rates, and of adult fecundity (all reproductive age-classes combined) were similar for the three species: adult survival consistently showed the highest elasticity, indicating that this demographic parameter has the

greatest potential influence on the population growth rate for these ungulates. For buffalo, the elasticity of adult survival was approximately 0.60, and 0.13 for calf survival and adult fecundity. Zebra and wildebeest showed similar values: the elasticities of adult survival were both 0.64, and the values for first-year survival and adult fecundity were 0.12 (for zebra) and 0.18 (for wildebeest).

The generation time ( $\bar{T}$ ) for the wildebeest population was the shortest ( $\bar{T} = 5.55$  years) and the zebras' the longest ( $\bar{T} = 8.24$  years) (Table 1.9), which is in agreement with our expectation that, for similar body sizes, population renewal rates in Perissodactyls are slower than in Artiodactyls.

Table 1.9. Demographic output of population functioning for buffalo, wildebeest and zebra models

Models	$\lambda$ (census)	$\lambda$ (model)	r	$\bar{T}$
Buffalo	1.063	1.052	0.051	7.56
Wildebeest	1.109	1.083	0.079	5.55
Zebra	1.011	1.010	0.010	8.24

$$\text{Natural rate of increase (r): } \sum \left( e^{-rx} l_x m_x dx \right) = 1$$

$$\text{Finite rate of increase: } \lambda = e^r$$

$$\text{Mean generation length: } \bar{T} = \sum \left( x e^{-rx} l_x m_x dx \right)$$

#### 4 - Simulating the effect of changing vital rates among species

When we replaced the zebra foal survival with estimates from the ruminants, the zebra population increased strongly (Fig. 1.2), with a  $\lambda$  varying from 1.010 to 1.085 and 1.102, respectively, with buffalo and wildebeest calf survival. When we replaced the calf survival of buffalo and wildebeest with the value for zebra foals, both the ruminant populations decreased, and the  $\lambda$ s declined from 1.052 to 0.982 for buffalo and from 1.083 to 0.975 for wildebeest.

When we replaced the reproductive rates of buffalo with the zebra values, the buffalo population increased faster, with  $\lambda$  increasing from 1.052 to 1.108. Conversely, when we replaced the reproductive rates of the wildebeest with zebra values, the wildebeest population increased more slowly, with its  $\lambda$  changing from 1.083 to 1.041. When we replaced the

reproductive rates of zebra with those of ruminants, the zebra population  $\lambda$  (1.010) declined to 0.972 (with buffalo values) or increased to 1.032 (with wildebeest values; Fig. 1.3).

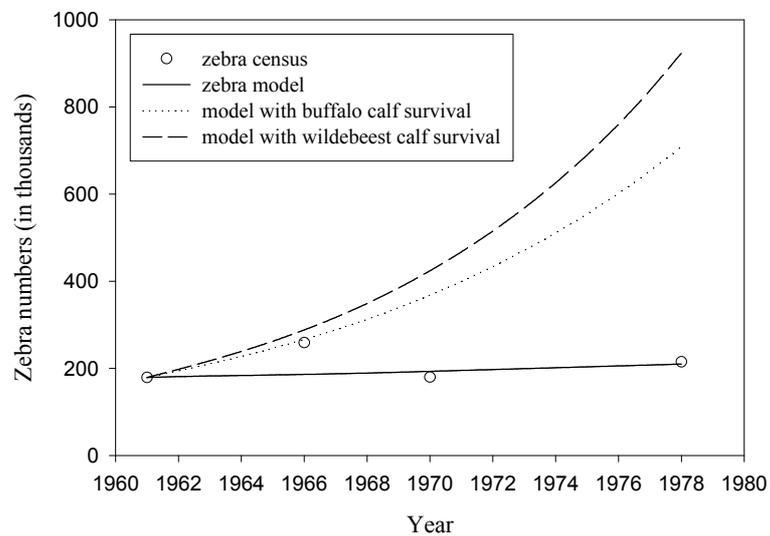


Fig. 1.2. Simulations of the zebra population using first-year survival values from the two ruminants

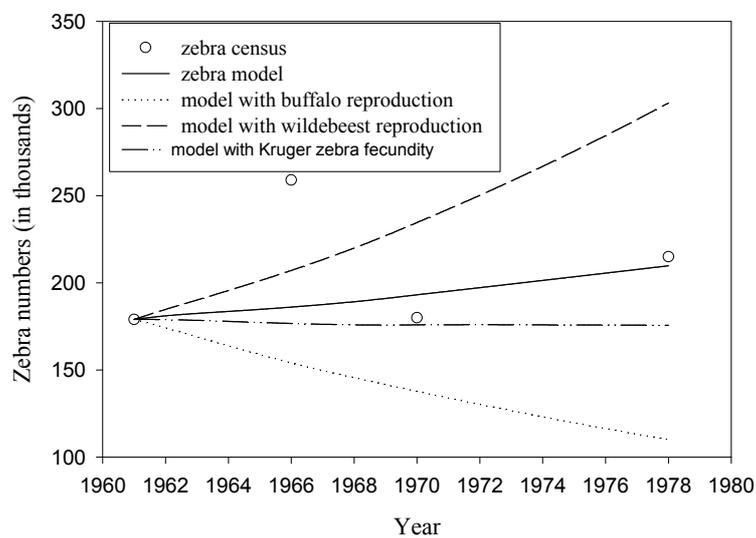


Fig. 1.3. Simulations of the zebra population using values of reproductive parameters from the two ruminants and from zebra in the Kruger National Park ( $f=0.79$ , in Smuts 1976a)

These simulations support the first prediction stemming from the predation hypothesis, that the differences in first-year survival between the zebra and the two ruminants are

sufficient to account for the observed constancy of zebra population size. The second prediction is rejected, as the reproductive parameters of zebra led them to increase faster than buffalo.

5 - Estimating the annual off-take of wildebeest, zebra and buffalo by lions and hyenas

The lions responded to the increase in the wildebeest population functionally and numerically. In the latter period wildebeest accounted for 41% of the kills, and the estimated numbers killed more than doubled, while the numbers of zebra killed changed very little (Table 1.6). There was little variation in the numbers of buffalo killed by lions between the two study periods.

The hyenas showed a functional response to the increase in both ruminant populations, showing a particularly strong response for buffalo which accounted for 10% of the hyena diet in the post-1975 period (Table 1.7). Between the two periods, the numbers of wildebeest killed more than doubled, whereas the numbers of zebra killed decreased slightly (Table 1.6).

As a consequence the estimated offtake of wildebeest by both predators more than doubled between the two study periods, from close to 22,500 in the pre-1970 period to 60,000 in the second period, accounting for about 5% of the wildebeest population in both periods. For buffalo the impact of lion and hyena predation more than tripled between the late 1960s and the 1980s, accounting for 5 and 10% of buffalo population, respectively.

The estimated numbers of zebra killed showed little change, from 16,100 to 16,400. Predation represented a higher proportion of the zebra population (about 8%) than of the wildebeest. Taking into account the potential number of newborn and the mortality of foals, yearlings and adults, we estimate that about 56,000 of the 200,000 zebra die each year. Natural predators therefore account for about 30% of the annual mortality of zebras.

#### **IV - Discussion**

The long-term studies conducted in the Serengeti provide data from which we have estimated rates of fecundity and survival, and built age-structured models for the three species

of ungulates. Our population models are based on similar age-classes so comparisons among the species are valid; and we can take into account the decrease in vital rates due to senescence, so the estimates of vital rates during the prime age stage should be unbiased (Loison *et al.* 1999; Festa-Bianchet *et al.* 2003). For the wildebeest model we used vital rates estimated at the beginning of their exponential increase (1962–1965), which could have led to an underestimation of the finite rate of increase during the accelerated increase which occurred after 1970. Nonetheless, the simulations derived from these deterministic models lead to patterns broadly consistent with the observed trends, so it is likely that the estimates of the vital rates are reasonably accurate. We discuss first the demographic processes involved, and then the ecological ones.

### 1 - Demographic processes

The values of the fecundity rates of the ruminants are similar to those in other populations (Gaillard *et al.* 2000a for a review), but the zebra values are high [e.g., the adult fecundity was 0.79 in the Kruger population (Smuts 1976a) compared with 0.88 here]. It is possible that the Serengeti value is overestimated, as the animals were shot by Game Department staff, without any particular procedure to avoid bias as in the other studies. However applying the Kruger value did not change the conclusions of our analysis: the zebra population was constant in size ( $\lambda=1.000$ ; Fig. 1.3). The reproductive values of zebra were not low enough to stop the increase in the ruminant populations, and the ruminant reproductive rates did not lead to a strong increase in zebra numbers. The differences in reproductive parameters (age at first reproduction and fecundity) among these species can therefore not account for the differences in population trends between the zebra and the ruminants. The differences found in reproductive traits appear mainly to reflect body size differences, as the reproductive potential of the zebra was intermediate between those of buffalo and wildebeest. The prediction that differences in life history traits between Perissodactyls and Artiodactyls contributed to the constancy of the zebra population size can therefore be rejected.

The only obvious difference in vital rates between the zebra and the ruminants concerns the first-year survival: the zebra value (0.389; Table 1.1) is about a half of that of the two ruminants and the upper limit of the confidence interval is below both ruminant values. This result is consistent with the value of 0.425 calculated for the Serengeti foals between 1962 and 1965 (from foal/mare ratios, Klingel 1969a).

The results of the simulations show clearly that with the ruminant first-year survival values, the zebra population would have increased fast, and with the zebra value, the ruminant populations would have declined. The difference in first-year survival alone is therefore sufficient to account for the difference in population kinetics observed between zebra and the two ruminant populations.

The results of the demographic analysis are therefore clear:

1. The hypothesis that the lower survival of foals is the key parameter for the zebra population dynamics and prevents an increase in zebra numbers is supported, and
2. The differences in life history traits between the zebra and the ruminants have no major effects on fecundity, and are clearly not sufficient to explain the differences in population dynamics, and the limitation of this zebra population.

## 2 - Ecological processes

By the 1980s the ruminants were limited by density-dependent intra- and interspecific competition (though buffalo were later limited by illegal hunting; Dublin *et al.* 1990; Mduma *et al.* 1999). If resource limitation is the key process in zebras too, survival should have been positively correlated with rainfall. The proportion of foals showed some variability (6–22% between 1980 and 1999), but was negatively correlated with rainfall (mean annual rainfall and dry season rainfall). This suggests that resource availability does not regulate recruitment and that during the wettest periods foals are more vulnerable. In the Kruger National Park, lions killed more zebra during wet periods (Smuts 1978; Mills *et al.* 1995), and this increase in prey vulnerability is probably due to fragmentation of the herds and an increase in grass cover for the lions. The proportion of yearlings varied between 7 and 25%. It was lower in the dry seasons, and increased with dry season rainfall (Table 1.9). This result suggests that in their second year, when most young zebras are weaned and must find their own food resources, survival may be influenced by the abundance of resources. Resource availability therefore appears to have both positive and negative effects on the survival of young zebra, in contrast to the situation in wildebeest, where the effects are clear and positive on the survival of young and adults (Mduma *et al.* 1999). Consequently there is little empirical evidence for “bottom up” limitation of the zebra population.

There are no data on the impact of diseases on the Serengeti zebras, but predation has been studied in detail. The lions switched to wildebeest after 1975 (41% of their diet compared with 20–25% in the 1960s, Table 1.5), but the numbers of lions increased and their off-take of zebras seems to have remained at about the same level throughout the period. The hyenas also switched to wildebeest, and particularly to buffalo after 1975, so the estimated number of zebra killed showed little change (Table 1.6). The combined impact of lions and hyenas on zebras represented about twice their impact on wildebeest. This could result simply from a difference in availability since zebra families disperse more widely than wildebeest (Maddock 1979; Sinclair 1985), which generally move together as a large herd, so the predation risk per individual is reduced (the “selfish herd”, Treisman 1975). As a consequence, wildebeest are, on average, available to lions 35% of the time, and zebra 63% (Schaller 1972).

Lion and hyena predation accounts for about 30% of the annual mortality of zebras, and could therefore have had a notable effect on the dynamics of the population, especially since this off-take by natural predators is additive to a similar number of zebras estimated to be killed by illegal hunting (19,000; Hofer *et al.* 1996). The data on the natural predators (their diets and numbers) were measured in the central part of the Serengeti, and extrapolation to the ecosystem as a whole is likely to be subject to error, so the results should be interpreted with caution. Nonetheless it seems safe to conclude that predation could have a more powerful effect on the zebra than the wildebeest in the Serengeti since the calculated impact on zebra is about twice that on wildebeest. The relative stability of the estimated off-take of zebras across the two periods indicates that predation could be the main limiting factor in spite of the considerable fluctuations in the numbers of natural predators. If this analysis is correct, the zebra were in a “predator pit”.

In plains zebra the gestation time is longer than a year (Smuts 1976a), so the minimum inter-foal interval is about 13 months (see Klingel 1969b). Consequently, zebra mares cannot foal in the same season each year and some foals are born in every month. Conversely, wildebeest and, to a lesser extent buffalo, show strong birth synchrony (Sinclair *et al.* 2000) with the majority of births occurring at the beginning of the wet season. Zebra foals are therefore available to predators for more of the year than wildebeest and buffalo calves, and are preferred prey in some ecosystems (see Cooper 1990; Mills and Shenk 1992). However, we calculate that some 60,000 zebra foals are born in the Serengeti each year. Lions and

hyenas eat more adult zebras than foals (Schaller 1972, Table 47; Kruuk 1972, Table 17; C. Packer, unpublished data; H. Hofer and M. East, unpublished data), so it is unlikely that predation by these species can account for the disappearance of nearly 38,000 foals.

In conclusion, we show here that the Serengeti zebras are limited by the high level of foal mortality. The effect of their particular life history traits on fecundity does not appear to be important, at least in this ecosystem. Predation by wild predators in addition to mortality caused by illegal hunting accounts for a large proportion of the mortality (about two-thirds), and could have a strong limiting effect on the zebra population; however, the processes involved in foal mortality have not been elucidated.

It has been proposed that a function of migration is to escape predation, and this model clearly fits the case of the wildebeest in the Serengeti (Fryxell *et al.* 1988). If predation is a major cause of zebra mortality, this analysis suggests that migratory zebra do not escape limitation by predators in this system: this could be because their very different pattern of habitat use leads them to be more widely dispersed than the wildebeest, and therefore more available to the predators (see Hofer and East 1995 for other cases where migratory species do not “escape predation”). The relatively high survival of calves in the buffalo, which are resident, can be explained by the highly effective collective defence of their young observed in this species (Prins 1996).

More detailed data on the causes of foal mortality in the Serengeti zebra, based on known individuals, are required to determine with certainty whether the process involved is predation, competition for resources, social limitation or pathogens. In particular it would be necessary to determine the nature and impact of the diseases and causes of malnutrition (*e.g.*, lack of milk, loss of mother due to predation or on migration, etc.). There is also the possibility that social factors contribute to zebra mortality: this does occur in equids (Berger 1986; Pluhacek and Bartos 2000). As is often the case in animal population dynamics, the answer may well be that it is a combination of these different processes.

### **Acknowledgements**

We thank the directors and boards of the Serengeti Wildlife Research Institute and Tanzania National Parks, the park wardens of Serengeti National Park. Without them none of the long-term studies on

Serengeti ungulates would have been possible. We thank the many colleagues that have improved the manuscript through their comments on early drafts, particularly N. Owen-Smith, H. Fritz, P. Inchausti, H. Kruuk, H. Klingel and two anonymous referees. This study was supported by the CNRS as part of the France-South Africa Programme International de Coopération Scientifique, Plant-Herbivore Dynamics in Changing Environments.

## Appendix 1.1

Calculations for zebra juvenile survival

Survival rates were estimated from the proportions of successive age-classes in the formulas below. As field observations were not done in the same month each year, we compared only samples obtained in 2 successive years (we included the comparison between January and November in 1994). For example, the yearling survival in 1988 was estimated from the juvenile proportion in the 1987 wet season and the yearling proportion in the 1988 wet season. For foal survival, we calculated the expected number of newborns in one year from the number of reproductive females in the previous year and their fecundity. To estimate first-year survival (Table 1.10), we compared the expected recruitment to the yearling class with the proportion of yearlings observed in the same year (Table 1.11).

Table 1.10. First-year survival

Year	Live foals (F)	Females of breeding age (B)	Expected live foals (Fe)	1 <sup>st</sup> year survival (s <sub>0</sub> )
t-1	$\frac{foals_{[t-1]}}{total_{[t-1]}}$	$\frac{adults_{[t-1]} \times p_a \times SR_f}{total_{[t-1]}}$		
t	$\frac{foals_{[t]}}{total_{[t]}}$	$\frac{adults_{[t]} \times p_a \times SR_f}{total_{[t]}}$	$B_{[t-1]} \times \sum_i (p_i \cdot f_i)$	$1 - \frac{Fe_{[t]} - F_{[t]}}{Fe_{[t]}}$

$p_a$  = proportion of adults >5 years old = 0.86

$SR_f$  = adult sex-ratio (female proportion) = 0.64

$p_i$  = proportion of adult females within age class i

$f_i$  = female fecundity within age class i

Table 1.11. Yearling survival

Year	Live foals (F)	Yearlings (Y)	Yearling survival (s <sub>1</sub> )
t-1	$\frac{foals_{[t-1]}}{total_{[t-1]}}$		
t	$\frac{foals_{[t]}}{total_{[t]}}$	$\frac{yearlings_{[t]}}{total_{[t]}}$	$1 - \frac{F_{[t-1]} - Y_{[t]}}{F_{[t-1]}}$

## Comments on Chapter 1

In this study we have demonstrated that low foal survival limits the Serengeti zebra population. However it is possible that variations in foal survival are density-dependent, which would lead to a “regulation” and not simply a “limitation” of the population. Unfortunately the demographic parameters used in our models were not derived from time-series (*i.e.* they were not estimated annually during our study period), and the game censuses of the Serengeti zebra population were irregular (4 aerial counts between 1961 and 1978). In this case it is difficult to test for density-dependent effects on vital rates. We therefore chose to use the term “limitation” in the text.

Because of the strong differences in population trends between zebra, buffalo and wildebeest, we would have expected major differences in the vital rates of these three species. Our study highlighted that only differences in first-year survival rates between these three ungulates are sufficient to explain the observed population trends. In such long-lived species, recruitment can significantly influence the population dynamics, but previous studies had not explicitly shown the importance of juvenile survival in the limitation of a zebra population.

The differences in vital rates (age-specific survival and fecundity) between our three species could not be tested through classical statistics using mean values and confidence intervals. It was therefore difficult to test the importance of such differences in the population dynamics of zebra, wildebeest and buffalo. We chose to swap vital rates between different species in order to examine consequences for their population growth rates. Such a method can be highly criticized if it is applied to species with very different body masses, because body mass constrains and influences species’ life histories. Since the three ungulates studied here are similar both in terms of ecology and body mass, we decided to swap demographic parameters to test their relative impacts on the population growth rates. Moreover the population dynamics of large mammals (and long-lived species) is generally characterized by a quasi-constant adult survival and a variable juvenile survival (Gaillard *et al.* 2000a), which means that juvenile survival is not species-specific and can vary greatly between populations. It is therefore not aberrant to swap such a parameter between our populations.

Finally, the method used to compare the relative impact of large predators on zebra, wildebeest and buffalo is based on rough calculations, and detailed numerical and functional

responses would have been helpful to assess the potential impact of lions and hyenas on the population dynamics of these three ungulates. Such data were unfortunately not available during our study period. To estimate the impact of predators on the population dynamics of Serengeti ungulates we would have to combine particular data on lion and hyena predation (such as the number of prey species killed within different sex and age classes across time) with accurate estimates on sex- and age-specific mortality in different prey species.

I have discussed here some critical comments that could be made on this comparative study of Serengeti ungulate population dynamics. Even if the ecological factor causing the relative stability of the Serengeti zebra population cannot be clearly identified, this study opens the discussion and helps us to think about the limiting factors acting on three Serengeti ungulates between 1960 and 1978. In particular, it points out the potential importance of predation in zebra population dynamics, which has often been considered as minor in the population dynamics of African ungulates although previously suggested by Sinclair (1985) in the particular case of the Serengeti zebra.

**Chapter 2:**  
**Bottom-up and top-down processes in African**  
**ungulate communities: resources and predation**  
**acting on the relative abundance of zebra and grazing**  
**bovids**

Sophie Grange & Patrick Duncan

Paper accepted in *Ecography*



## **Abstract**

African ungulate populations appear to be limited principally by their food resources. Within ungulate communities, plains zebras coexist with grazing bovids of similar body size, but rarely are the dominant species. Given the highly effective nutritional strategy of the equids and the resistance of zebras to drought, this is unexpected and suggests that zebra populations may commonly be limited by other mechanisms. Long-term research in the Serengeti ecosystem and in the Kruger National Park suggests that zebra could be less sensitive to food shortage, and more sensitive to predation, than grazing bovids: if this is a general principle, then, at a larger scale, resource availability should have a weaker effect on the abundance of zebra than on grazing ruminants of similar body size (wildebeest and buffalo), and zebras should be relatively more abundant in ecosystems where predators are rare or absent. We test these expectations using data on 23 near-natural ecosystems in East and Southern Africa. The abundance of wildebeest is more closely related to resources than is that of zebra; buffalo are intermediate. We show that hyena densities are closely correlated with those of lions, and use the abundance of lions as an index of predation by large predators. The numerical response of lions to increases in the abundance of their prey was linear for mesoherbivores, and apparently so for the three species alone. Finally, the abundance of zebra relative to grazing bovids is lower in ecosystems with high biomasses of lions. These results indicate that zebras may commonly be more sensitive to top-down processes than grazing bovids: the mechanism(s) have not been demonstrated, but predation could play a role. If it is true, then when numbers of the large mammalian predators decline, zebra populations should increase faster than buffalo and wildebeest.

## I - Introduction

In some near-natural African savanna ecosystems which have not been greatly altered by human activities in the last centuries, large mammals are both diverse and abundant. Medium-sized ungulates constitute a major part of the vertebrate biomass (Cumming 1982) and therefore play an important role in the structure and the functioning of these ecosystems. The ecological impact of these herbivore communities depends on their abundance and also their species composition: it is now widely accepted that their abundance is determined principally by the abundance of their food resources (Coe *et al.* 1976, East 1984, Fritz & Duncan 1994). The species composition of ungulate communities results from the interaction of several processes which influence the dynamics of coexisting populations. “Bottom-up” processes depend on the food resources (both quantity and quality) whereas “top-down” processes involve natural enemies (predators, and also diseases). Both types of processes shape ungulate communities, and their respective impacts can vary between different ecosystems.

Among medium-sized grazing herbivores, equid and bovid species are important components of these communities. Convergent evolution has led these 2 families to acquire similar adaptations to life in open savannas, and equids have highly effective foraging strategies which can allow them to out-compete ruminants (Duncan *et al.* 1990, Ménard *et al.* 2002). Indeed, in the reserve of Oostvaardersplassen in the Netherlands, cattle and horses have been left unmanaged since the 1980's and have reached relatively high densities. In this ecosystem without large predators, Konik horses showed a higher intrinsic rate of population increase compared to Heck cattle (Vulink 2001, T. Vulink pers. comm. April 2004), and currently outnumber the cattle which apparently are regulated by food shortage in winter. In Africa, plains zebra (*Equus quagga*) and grazing ruminants coexist widely, but bovids such as blue wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*) are clearly more successful, since one of these species dominates the guild of grazing ungulates in most near-natural African savanna ecosystems (87% of those studied here). Consequently, the processes limiting the abundance of zebra and grazing bovids of similar body size are of particular interest: we focus this study on buffalo and wildebeest, which use similar resources to the zebra. In the Serengeti the wildebeest and buffalo populations are limited by their food supply (Sinclair 1977, Mduma *et al.* 1999), whereas zebra are limited by their low juvenile survival. The cause of the high foal mortality in this ecosystem is not known, but it has been suggested that it could be predation (Grange *et al.* 2004). In Kruger National Park, where annual rainfall

did not have a direct effect on zebra survival rates, it has been suggested that lion predation could have an effect on survival rates of immature zebra (Owen-Smith *et al.* 2005). On the other hand, in Laikipia, where large mammalian predators are not abundant, zebras are limited by their food resources (Georgiadis *et al.* 2003).

These results indicate that there are important differences among ecosystems in the factors which regulate zebra populations, and that predation may play a major role. Since the abundance of predators and of resources varies among ecosystems we test the hypothesis that the abundance of equids shows a different response to these variables, compared to wildebeest and buffalo. We use census data from 23 near-natural ecosystems in East and Southern Africa, in the 1990s. We first analyse the influence of the quantity and quality of food resources on the abundance of these species using rainfall and soil nutrient availability as proxies: from previous studies we expect positive effects on herbivore biomasses, and expect the abundance of the grazing bovids to be more tightly determined by food resources than zebra. We then examine the relationships between the abundance of medium-sized ungulates and of large predators, and test the hypothesis that the ratio “zebra / grazing bovids” declines as predator biomass increases.

## **II - Material and methods**

### 1- Protected areas

We established a database which includes protected areas in East and Southern Africa where data are available on the abundance of the herbivores and their predators (Appendix 2.1). To avoid biases due to predation by people we included only near-natural areas which are effectively managed: this selection was based on information in the UNEP-WCMC website (<http://quin.unep-wcmc.org>; Table 1), completed for a few areas with information published elsewhere (Lake Manyara, Serengeti, Kruger, Etosha and Ngorongoro Crater). Among the 81 areas we examined, 4 where poaching focused on megaherbivores (elephant and rhino; Ruaha, North and South Luangwa, and Tarangire) were included as this study concerns mesoherbivores. Ninety-one percent of the 23 protected areas we retained are classified in IUCN category “II” (National Park). Ngorongoro Crater is in category “VI” (Management Area), and Selous in “IV” (Nature Reserve), but they are as well protected as the National

Parks. Sixteen of these areas are > 1000 km<sup>2</sup>, the other 7 are 100 - 1 000 km<sup>2</sup> (see Appendix 2.1).

The mean annual rainfall for each area was derived from a global model based on monthly measurements of rainfall between 1980 and 1999 (Willmott & Matsuura 1998). The geographical coordinates of each site were obtained from the UNEP-WCMC website (<http://quin.unep-wcmc.org>) and the estimates were compared with published measurements where available; the data from the two sources differed by >50% for Amboseli (Coe *et al.* 1976), Hluhluwe-iMfolozi (Coe *et al.* 1976), Mikumi (UNEP-WCMW website), Selous (Bell 1982) and Tsavo (Coe *et al.* 1976), so we used the published rainfall data in these cases.

The soil nutrient availability (SNA) in each area was determined from a geological map (Clark 1967, in Bell 1982): “high” SNA for volcanic and marine sediments, “medium” for rift valley and cratonic sediments, and “low” for basement, granite and Kalahari sands (for more information see Bell 1982).

## 2 - Animal data

Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) are the main predators of medium-sized ungulates in these ecosystems. Lion and hyena densities were obtained from reports (East 1997a, 1997b, Mills & Hofer 1998, Bauer & Van der Merwe 2002, and Chardonnet 2002), papers (Sinclair & Arcese 1995, Caro 1999, Du Toit *et al.* 2003, and Kissui & Packer 2004), theses (Bonyongo 2004), and a personal communication (N. Drouet-Hoguet 2005 for Hwange). These were based on field studies (60% and 100% of lion and hyena data respectively) or on expert opinion, based on comparisons with densities measured in neighbouring or similar situations (40% of the lion data); data on lion were available for 18 areas, and on hyena for only 10. There is a significant relationship between lion and hyena biomasses:  $\log_{10}(\text{HyenaBIOMASS}) = 1.0794 \times \log_{10}(\text{LionBIOMASS}) - 0.0247$  ( $n = 10$ ;  $R^2 = 0.7092$ ;  $p = 0.0022$ ; Shapiro test:  $W = 0.8914$ ,  $p = 0.1758$ ). We therefore consider that lion biomasses are a good indicator of the abundance of large predators (both lions and spotted hyenas), and use data on lions only in the analyses.

Data on ungulate population sizes were compiled from IUCN reports (East 1996a, 1996b, 1997a, 1997b, 1997c, 1999, Moehlman 2002), theses (Bonyongo 2004), published

papers (Dublin *et al.* 1990, Du Toit *et al.* 2003, Mduma *et al.* 1999, Prins & Douglas-Hamilton 1990, Sinclair 1977, Sinclair & Norton-Griffiths 1979, Sinclair & Arcese 1995), reports (Zimbabwean Parks and Wildlife Management Authority and WWF for Hwange NP), and a personal communication (Sue Van Rensburg for Hluhluwe-iMfolozi). Data from five protected areas where no lion data were available were included to increase the sample size for the analyses of the effect of variations in resource availability. Most of the censuses were aerial counts (83%), but ground counts were used for Hluhluwe-iMfolozi, Lake Manyara, Lake Nakuru, and Nairobi. Censuses are of course subject to errors (bias and precision), but these are likely to induce noise rather than pattern. We used ungulate censuses conducted in the same decade as the estimates of lion numbers, generally the 1990s (Table 2.1). Populations of large herbivores in some of these areas have varied: in order to obtain representative population sizes comparable with the predator data, we chose periods of relative stability as close as possible to the dates of the predator estimates. In 8 of the 23 near-natural areas several annual population censuses were available (Hluhluwe-iMfolozi, Hwange, Kruger, Lake Manyara, Nairobi, Ngorongoro Crater, Okavango, and Serengeti). We therefore estimated population growth rates ( $r$ ) and considered that populations were sufficiently stable when  $r < 10\%$  (noted as S, S/I or S/D in Table 2.1). For the other areas we used the IUCN reports, and as far as possible retained periods when the populations were classed as stable: 83% of the populations of the 3 species in the 23 areas were stable during our study periods (see Table 2.1). The periods used for ungulate and predator censuses do not always overlap, but never differ by more than 9 years (mean = 4.8 years; range = 0-9). This temporal difference could not affect the results strongly, given the stability of the ungulate populations.

Most of the prey of lions are “mesoherbivores” (ungulates weighing 10-1000 kg), so we restricted the analysis to this set of ungulates (giraffes were not included). To determine ungulate and lion biomasses ( $\text{kg}/\text{km}^2$ ), data on body weights were obtained from a compilation of published data (cf. Appendix 2.2). We used the mean population body weight – i.e.  $\frac{3}{4}$  of female body weight (Owen-Smith 1988).

### 3 - Statistical analyses

As lion biomass and rainfall are collinear (log10 transformation,  $r = 0.6531$ ,  $p = 0.0033$ ), we have analysed the effects of resource availability (“rainfall” and “SNA”) and of

lion biomass on the relative abundances of medium-sized herbivores separately. The linear models were tested with the Shapiro test for the normality of residuals.

### 3.1 - *The effect of rainfall and soil quality on ungulate biomasses*

To test for effects of resource availability on ungulate biomasses, we performed analyses of covariance with R-software ([www.r-project.org](http://www.r-project.org)). The ungulate biomasses were normalized with a  $\log_{10}(x)$  transformation, and the homogeneity of their variances among the classes of soil richness was assessed using Bartlett's test (K-squared = 2.1869, d.f. = 2,  $p = 0.3351$  for mesoherbivores; K-squared = 1.771, d.f. = 2,  $p = 0.4125$  for zebra; K-squared = 0.8903, d.f. = 2,  $p = 0.6407$  for buffalo; and K-squared = 0.1922, d.f. = 2,  $p = 0.9084$  for wildebeest). The analyses were performed for each species using only the protected areas where they occurred (23 areas for mesoherbivores and zebra, 21 for buffalo, and 17 for wildebeest; cf. Appendix 2.1).

### 3.2 - *Predation*

We examined the numerical responses (see Messier 1994) of lions to the abundance of mesoherbivores, and also to zebra, wildebeest, and buffalo. We first used a non-parametric smoothing program based on locally weighed regressions (LOWESS program; in Crawley 2002) to describe the general tendency of our different numerical responses. The results suggested linear relationships, but with a break in the line. We therefore compared linear and non-linear responses and selected the best model. We used non-linear regressions which can allow a threshold in the numbers of the lions at higher prey biomasses: the model was  $y = \frac{b \times x}{a + x}$  where  $y$  represents lion biomass,  $x$  is prey biomass,  $b$  is the asymptote, and  $a$  is the value of prey biomass for the lion biomass reaches 50% of the asymptotic value. To estimate the goodness of fit of these regressions, we calculated the % of variance explained by the linear regression of predicted on observed values.

Food selection by lion is described for 5 sites (Etosha, Kruger, Lake Manyara, Ngorongoro Crater, and Serengeti) where data on lion diets were available, by comparing the proportions of zebra, wildebeest, and buffalo in the lion diet with their proportions in the prey populations.

The ratio of “zebra / buffalo and wildebeest” (Z/BW, biomasses) was used to examine the relative abundances of these 3 ungulate species in relation to lion biomass. We used a log10 transformation for our variables (Z/BW ratio and lion biomass) and checked the normality of the residuals.

### III- Results

#### 1 - Rainfall and soil quality

The mesoherbivore model accounted for 72% of the variance (additive model:  $F_{3;19} = 16.65$ ;  $p = 1.5 \times 10^{-5}$ ) and as expected, mesoherbivore biomass increased with rainfall ( $F_{1;19} = 20.266$ ;  $p = 0.0002$ ) and SNA ( $F_{2;19} = 14.842$ ;  $p = 0.0001$ ). The buffalo model accounted for almost half of the variance in the abundance of this species (44%,  $p = 0.0276$ ), with biomass lower on low nutrient soils (349 kg/km<sup>2</sup>) than on medium and high (1967 and 2326 kg/km<sup>2</sup>), and also increasing with rainfall ( $p = 0.0453$ ; Table 2.2). The abundance of wildebeest increased with SNA ( $p = 0.0011$ ) and tended to increase with annual rainfall, but not significantly ( $p = 0.0848$ ; Table 2.2). The model accounts for 68% of the variance and wildebeest biomasses were much higher in ecosystems with high SNA (2784 kg/km<sup>2</sup>) compared to medium and poor soils (115 and 48 kg/km<sup>2</sup>).

For zebra, the model was significant (additive model:  $p = 0.0364$ ), but explained only 35% of the variance: annual rainfall had no significant effect ( $p = 0.2210$ ), but there was an effect of SNA ( $p = 0.0267$ ; Table 2). As in wildebeest, the abundance of zebra was much higher in areas with high SNA than elsewhere (the mean biomasses were 172, 242 and 1040 kg/km<sup>2</sup> on low, medium, and high SNA respectively).

Table 2.2 – Analyses of covariance of ungulate biomasses with one covariate (mean annual rainfall) and one factor (SNA). Significance codes: \* < 0.05, \*\* < 0.01, \*\*\* < 0.001.

Species	Rain		SNA		Model		
	F (df)	p	F (df)	p	F (df)	P	R <sup>2</sup>
Buffalo	4.6657 (1;17)	0.0453 *	4.4665 (2;17)	0.0276 *	4.5330 (3;17)	0.0165 *	0.4444
Wildebeest	3.4811 (1;13)	0.0848	12.1311 (2;13)	0.0011 **	9.2480 (3;13)	0.0015 **	0.6809
Zebra	1.6013 (1;19)	0.2210	4.4127 (2;19)	0.0267 *	3.4760 (3;19)	0.0364 *	0.3543

2 - Predation

The biomasses of both lions and ungulates in the Ngorongoro Crater were considerably higher than in the other areas; this point is an outlier and has therefore been removed from all our numerical responses. The abundance of lions increased with the biomass of mesoherbivores: the best model was a linear regression which explained 60% of the variance ( $b = 0.0019$ ,  $p = 0.0003$ ; Shapiro test:  $W = 0.9402$ ,  $p = 0.3211$ ; Fig. 2.1). The abundance of lions therefore increased with that of their prey, within the range 0-9,000 kg/km<sup>2</sup>, and the data from Ngorongoro fitted the pattern of the other points.

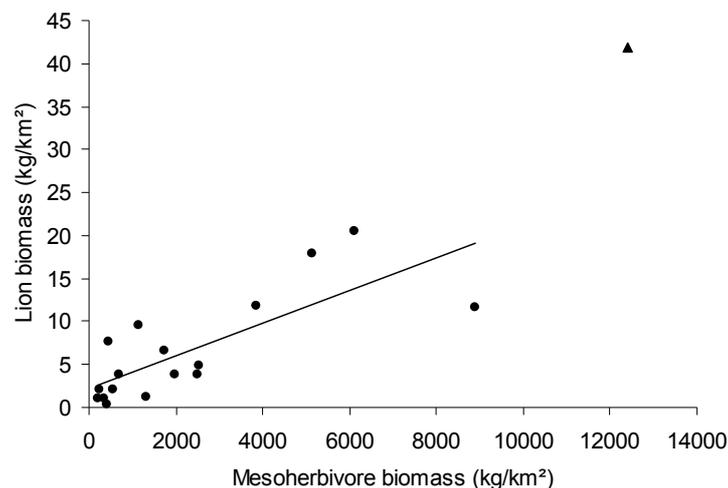


Figure 2.1 – The linear numerical response of lions to mesoherbivore biomass across 17 protected areas, excluding the outlier, Ngorongoro Crater, represented by a black triangle: ( $p = 0.0003$ ;  $R^2 = 0.60$ ).

The patterns for the different species were rather similar: lion numbers increased with wildebeest and tended to do so with zebra and buffalo biomasses (Fig. 2.2). For wildebeest, the best model was linear ( $p = 0.0397$ ,  $R^2 = 0.3585$ ; Shapiro test:  $W = 0.9099$ ,  $p = 0.2130$ ); the zebra and buffalo models were not significant (respectively  $p = 0.1256$ ,  $R^2 = 0.1492$ ; and  $p = 0.0607$ ,  $R^2 = 0.2450$ ).

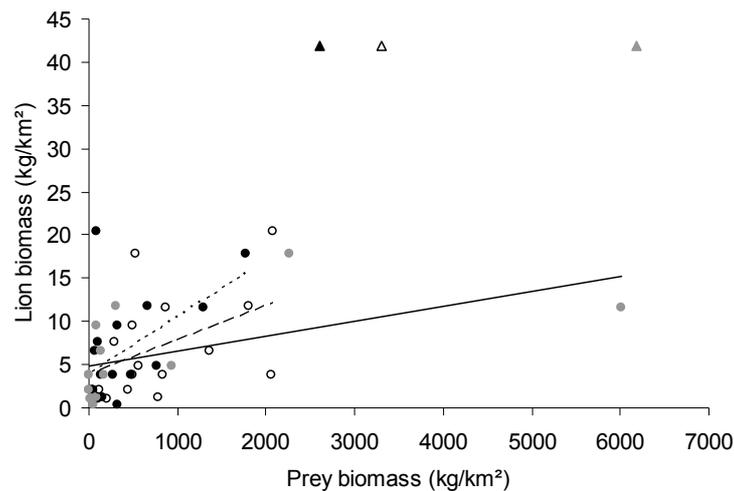


Figure 2.2 – The numerical responses of lions to the biomasses of three prey species: zebra (black circles; dotted line), wildebeest (grey circles; solid line) and buffalo (open circles; dashed line). The linear models for zebra and buffalo are indicated, but are not significant. The points representing the outlier, Ngorongoro Crater, figure as triangles.

Preferences for the 3 species of prey were compared using linear regressions through the origin of the proportion of different prey in lion diets and in the mesoherbivore community (measured in numbers, not biomass; Fig. 2.3) in the few areas where data were available (Etosha, Kruger, Lake Manyara, Ngorongoro Crater, and Serengeti). The slopes of the regressions for the bovids tended to be weaker than the slope for the zebras, but did not differ significantly from the diagonal (Kolmogorov-Smirnov test:  $D = 0.2$  and  $p = 1$  for zebra;  $D = 0.4$  and  $p = 0.873$  for wildebeest;  $D = 0.25$  and  $p = 1$  for buffalo).

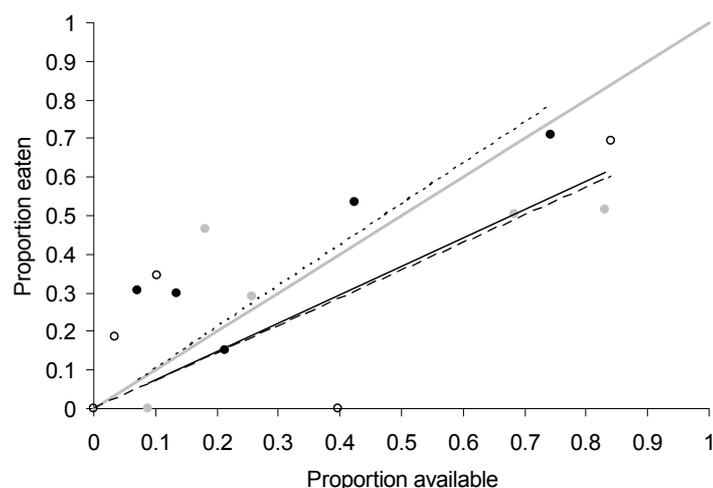


Figure 2.3 – The proportions of zebra (black circles and dotted line), wildebeest (grey circles and solid line) and buffalo (open circles and dashed line) in the ecosystems and in the lion kills. The proportions are based on numbers of kills, not biomass; the regression lines were forced through the origin; the grey line is the diagonal.

Zebras were the dominant grazing herbivore in 2 systems, Makgadikgadi and Etosha, which had low densities of lions (biomass < 1kg/km<sup>2</sup>); and across the 18 areas, the ratio of zebras to wildebeest and buffalo decreased significantly as lion biomass increased (linear regression:  $b = -0.5204$ ,  $p = 0.0370$  and  $R^2 = 0.2444$ ; Shapiro test:  $W = 0.9625$ ,  $p = 0.6503$ ; Fig. 2.4). There was no effect of rainfall on the Z/BW ratio (linear regression:  $b = -0.0004$ ,  $p = 0.4840$  and  $R^2 = 0.0261$ ; Shapiro test:  $W = 0.9563$ ,  $p = 0.4449$ ).

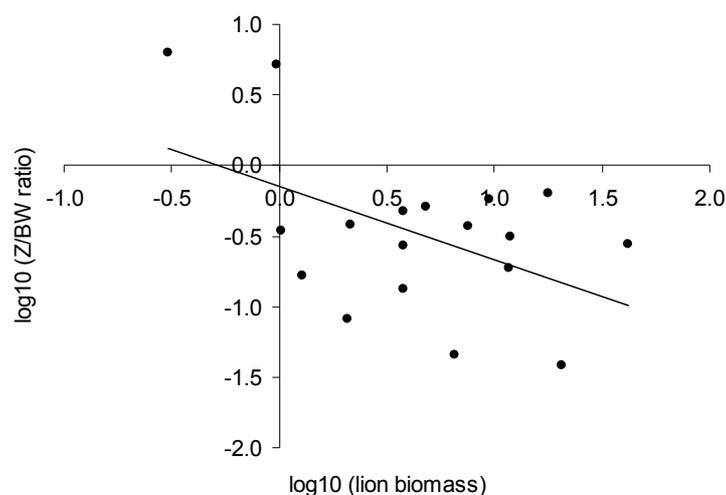


Figure 2.4 – Linear regression of the ratio of zebra to the sum of the biomasses of buffalo and wildebeest in relation to lion biomass in 18 protected areas:  $p = 0.0370$ ;  $R^2 = 0.2444$ .

#### IV - Discussion

The buffalo model, which explained 44% of the variance in the abundance of this species, indicated a limiting effect of food resources – both in terms of quantity and quality. Sinclair (1977) has already shown for 12 East African parks that buffalo density in the 1960s and 1970s increased with mean annual rainfall, and we show here that buffalo are much less abundant on low nutrient soils than on the other types.

Wildebeest were abundant only on rich soils: this difference with buffalo is not surprising as wildebeest are much smaller (wildebeest females weigh 163 – 180 kg; buffalo females weigh >500 kg, Appendix 2.2), and therefore require higher quality forage. Wildebeest survival in the Serengeti is limited by dry season rainfall (Mduma *et al.* 1999), so it is

surprising that the abundance of this ruminant was not affected by rainfall. This is perhaps because the range of rainfall in our sites was small (there are no sites with rainfall < 300mm in the database), and we did not separate dry and wet-season rainfall.

The pattern observed here, which suggests that grazing bovids generally are food-limited, is consistent with the few fine-grained studies of the dynamics of ungulate populations (in particular the buffalo and wildebeest populations in the Serengeti ecosystem [Sinclair 1977, Mduma *et al.* 1999], although there are exceptions, as wildebeest are limited by disease and predation in Etosha [Gasaway *et al.* 1996]). This study therefore confirms a previous analysis of data collected before 1980, that the main factor limiting the abundance of African ungulates is their food resources, both in amount (via rainfall) and quality (via soil richness; see Fritz & Duncan 1994).

Though the range of rainfall studied here had no significant effect, resource quality has some effect on the abundance of zebras, which were more abundant on rich soils. However, the model accounted for only 35% of the variance in zebra biomasses, which indicates that other factors than resources were more important in determining variations in zebra biomass across ecosystems. This result is consistent with observations during the 1973 drought in Nairobi National Park, that hartebeest (*Alcelaphus buselaphus*) and wildebeest were affected by food shortage more than the zebra (Hillman & Hillman 1977). In Kruger Park too, zebras appear to be less affected by water availability than were grazing ruminants (Redfern *et al.* 2003).

Lion populations responded positively to the biomass of mesoherbivores with a linear response in at least the range 0-9,000 kg/km<sup>2</sup>, suggesting that lions generally were limited by prey biomass. Lions can be limited by severe disease outbreaks, as occurred in the Ngorongoro Crater (Kissui & Packer 2004); this effect appeared to be density-dependent, and occurred when the density was > 400 lions/1000 km<sup>2</sup>. The numerical response we have found across ecosystems is consistent with their response in the Serengeti ecosystem to the strong increase in the numbers of ruminants in the 1970s; lion and hyena numbers increased by 100 and 135%, respectively, between the early 1970's and 1990's (C. Packer pers. comm.2004, Hofer & East 1995). More generally, the community of large mammalian predators in African savannas shows an apparently linear numerical response to increases in the abundance of large herbivores (East 1984).

The lion numerical response may be linear for wildebeest; one data point (the Serengeti, bottom right corner of the graph) is very low, which is not surprising as the migration in the Serengeti ecosystem reduces the availability of wildebeest to lions (Mduma *et al.* 1999). Lions tend to increase with zebra and buffalo numbers too, but not significantly. These apparently linear numerical responses for different prey species and for the ungulate community mean that lion populations do not show saturation. Interestingly the abundance of lions is unrelated to the diversity of the prey community (multiple regression with mesoherbivore biomass and H;  $R^2 = 0.6538$ ,  $p = 0.0001$  for mesoherbivore biomass, and  $p = 0.4388$  for H, where H is the Shannon index of diversity). This result implies that the abundance of prey is more important than the species composition of the community for this generalist predator.

The linear numerical response of lions to increases in the abundance of their prey allows them to reach high densities, over 100 lions per 1000 km<sup>2</sup> in Lake Nakuru, Nairobi, Kruger, Hluhluwe-iMfolozi, and the Serengeti ecosystems and over 400 lions per 1000 km<sup>2</sup> in Ngorongoro Crater. This is in striking contrast to the non-linear response of another mammalian predator, the wolf (*Canis lupus*), to their main prey, moose (*Alces alces*). Wolf numbers increase sharply at low moose densities and then reach a plateau at about 60 wolves per 1000 km<sup>2</sup> (Messier 1994), presumably limited by social behaviour. In wolf societies, the alpha female breeds and subordinate females are non-breeding helpers (Mech 1970); in lion societies, all females in the pride can breed. Though there is no evidence for a limiting effect of social behaviour in lion populations, disease may come into play when densities are very high (Kissui & Packer 2004).

The limited data available on lion diets in relation to the availability of the different prey species show no evidence for consistent selection or avoidance of any of these three ungulates. There is a suggestion that the two bovids may have been under-used, which apparently was not the case for zebras.

The Z/BW ratio declined with increasing lion biomasses. Zebras were more abundant than grazing bovids in only 2 of these ecosystems, Etosha and Makgadikgadi, which had very low densities of lions, and thus a low predation pressure on medium-sized ungulates. This effect is unlikely to be an artefact due to a negative correlation between zebra and grazing bovid biomasses since these are positively correlated:

$\log_{10}(Zbiomass) = 0.3964 \times \log_{10}(BWbiomass) + 1.1943$  ( $p = 0.0074$ ;  $R^2 = 0.2951$ ; Shapiro test:  $W = 0.9408$ ,  $p = 0.1868$ ). Further rainfall had no effect on the ratio (see above Results).

Though this model explains only 24% of the variance in the relationship between lions and the Z/BW ratio, it suggests, as expected, that predation had a stronger effect on zebras than on grazing bovids. The mechanism could be a greater availability of zebras compared to wildebeest, spatially and temporally. The spatial distribution of wildebeest is more clumped: this is very clear in Serengeti (Maddock 1979), but it is also true in dystrophic ecosystems (Redfern *et al.* 2006). Since the minimum inter-foal interval in zebras is 13 months (Klingel 1969b), zebra mares cannot produce successive foals in the same season, and zebra foals are available to predators throughout the year. Conversely, wildebeest and, to a lesser extent buffalo, show strong birth synchrony (Sinclair *et al.* 2000) with the majority of births occurring at the beginning of the wet season.

Although predator-prey relationships at the local scale are clearly variable, this analysis at a regional scale suggests that there is a general principle: zebra are more strongly influenced by lion predation than are these grazing bovids. An experimental approach would of course be ideal to demonstrate this: since this obviously is not feasible, analysis of long-term data sets on ungulate population trends before and after important variations in predator densities (due to removals or disease outbreaks) would be a useful test of this principle.

In this paper we have considered the effects of variations in resources and predation on the abundance of these species, but other factors we have not been able to consider here, such as parasites, diseases, and social factors, may play important roles too. Little information is available on the impact of diseases on zebra population dynamics: anthrax was reported during the 1990's in Etosha, Kruger, South Luangwa, and Tarangire (Moehlman 2002). However, anthrax affects bovids too, and there is no suggestion that zebras are more sensitive to this disease. Equine diseases have been reported in Kruger and Nairobi (African Horse Sickness), and Etosha (Equine Encephalosis Virus), but zebra are not known to show clinical effects, and zebra biomasses are not particularly low within these parks. Social factors are another possibility: infanticide has been noted in captive plains zebra (Pluhacek & Bartos 2000), as well as in wild horses (Berger 1986), but not yet in zebras in the wild.

In conclusion, this study has clarified the interactions between large mammal herbivores, their resources, and their predators in savanna ecosystems. The relative abundances of zebra and grazing bovids vary widely among ecosystems, and result from the action of “top-down” and “bottom-up” ecological processes whose strength varies. First, wildebeest, as expected, appeared to be more closely tied to the resources than were zebra; buffalo were intermediate. The abundance of hyenas was closely and positively correlated with that of lions. The numerical response of lions, our proxy for predation pressure, to mesoherbivores was close to a type I (linear), so it is possible that their densities are limited by prey availability, at least until they reach very high densities. Zebras were more abundant than wildebeest and buffalo in ecosystems with low lion densities. The mechanism involved may not simply be a selection for zebras, but could be linked to their greater spatial and temporal availability. The results of this study suggest that the role of predation is particularly important for zebras; if this is true, in ecosystems where predator numbers (particularly lions) decline strongly (*e.g.* as a result of predator control), zebras should increase faster than grazing bovids.

### **Acknowledgements**

Norman Owen-Smith and Jean Clobert have been generous with their ideas and time in many discussions on the factors limiting ungulate communities. We thank Fabrice Hibert for his help with the African Antelope Database 1998, and Craig Packer for his data on lion diet in the Serengeti. We are also very grateful to C. Bonyongo for the censuses in the Okavango delta (Botswana), and to M. Valeix, H. Fritz and N. Drouet-Hoguet for providing the data on ungulates and hyenas in Hwange National Park (Zimbabwe). We also thank Sue Van Rensburg and the Earthwatch Institute for respectively providing and funding the censuses conducted in Hluhluwe-iMfolozi. This manuscript has been largely improved by the critical comments of four referees.

Chapter 2

Table 2.1 – Information on the 23 African protected areas selected for this study. The period indicated for ungulate censuses is the whole period and can vary between species. Notes for population trends: S = stable, D = decreasing, I = increasing.

Protected area	Perturbations (source : UNEP-WCMC web site, other publications see <i>Methods</i> section)	Period for data used		Population trends			
		Ungulates	Lion	Hyena	ZB	WB	BU
Amboseli		1991-1996	2001	no data	S	S	S
Etosha	Fences stop migrations, anthrax + lion contraception (1986)	1995	1991	1979-1986	S	S	S
Hluhluwe-iMfolozi	Fenced	1991-1998	2002	1975-1981	S/I	S	S
Hwange	Artificial waterholes	1990-1999	2001-2002	2004	S/D	S/I	S/I
Katavi	Some poaching	1991-1995	2002	1996	I	S	S/D
Kruger		1980-1993	2002	1984	S/I	S	S
Lake Manyara	Rinderpest (1959), anthrax (1984), fences	1959-1990	no data	no data	S/I	S/I	S
Lake Mburu		1995	no data	present; no data	D	S	S
Lake Nakuru	Water pollution	1990-1995	1997-2002	no data	?	I	I
Luambe		1994	no data	no data	S	S	S
Makgadikgadi-Nxai Pan		1994	2001	no data	D	S/I	S
Mana Pools		1995	2002	no data	S	S	S
Mikumi	Some poaching and grazing, a highway in Park	1994	no data	no data	D	S/D	S
Nairobi	Fences stop migration + buffalo introduced	1990-1995	2001	1976	S	S	S/D
Ngorongoro Crater	Some poaching, disease in lions & malignant catarrh in wildebeest	1963-1992	1962-1998	1966-1968	S	S	S/I
North Luangwa	Some poaching on elephant and rhino	1995	2002	no data	S	S	I
Okavango		1989-2002	1990-2002	1991-1999	S/D	S/I	S
Ruaha	Heavy poaching on rhino	1993-1996	2002	no data	S	S	D
Selous	Some poaching	1994	2002	1994	I	S	I
Serengeti	Rinderpest (1960s), some poaching (1980s)	1971-1996	1991-2002	1967-1991	S	S	S/D
South Luangwa	Some poaching on elephant and rhino	1994	2002	no data	S	S	S
Tarangire	Fences stop migration, poaching on black rhino	1994	no data	no data	S	S	S
Tsavo	Some poaching, highway + railway in Park	1991-1997	1991-2002	no data	S/D	S	D

**Appendix 2.1: The database on 23 African protected areas: IUCN category, area size (km<sup>2</sup>), mean annual rainfall (1980-99), soil nutrient availability and the biomasses of medium-sized ungulates and their predators (kg/km<sup>2</sup>).**

Protected area	Country	IUCN	Area (km <sup>2</sup> )	SNA	Rainfall (mm)	Mesoherbivores (kg/km <sup>2</sup> )	Zebra (kg/km <sup>2</sup> )	Wildebeest (kg/km <sup>2</sup> )	Buffalo (kg/km <sup>2</sup> )	Lion (kg/km <sup>2</sup> )	Hyena (kg/km <sup>2</sup> )
Amboseli	Kenya	II	392	high	350	2523.62	769.80	933.67	562.04	4.85	no data
Etosha	Namibia	II	22270	low	354	206.49	96.53	18.67	0.00	0.98	2.43
Hluhluwe-Umfolozi	South Africa	II	965	medium	650	3846.57	660.81	312.95	1809.30	11.81	22.56
Hwange	Zimbabwe	II	14651	low	549	228.61	49.18	5.84	122.68	2.15	3.21
Katavi	Tanzania	II	13000	medium	1055	2489.89	270.70	0.00	2054.82	3.80	7.39
Kruger	South Africa	II	21682	low	697	1158.00	326.79	78.14	488.31	9.50	7.09
Lake Manyara	Tanzania	II	110	high	895	7497.98	217.84	204.41	6799.68	no data	no data
Lake Mburo	Uganda	II	1563	low	1021	667.27	254.97	0.00	207.29	no data	no data
Lake Nakuru	Kenya	II	139	high	928	6129.71	80.22	0.00	2082.30	20.50	no data
Luambe	Zambia	II	320	medium	900	8652.72	241.00	16.88	8301.56	no data	no data
Makgadikgadi-NxaiPan	Botswana	II	20000	low	329	411.32	326.42	52.35	0.00	0.30	no data
Mana Pools	Zimbabwe	II	2162	medium	706	562.05	36.08	0.00	441.63	2.08	no data
Mikumi	Tanzania	II	3215	medium	750	613.94	51.01	44.78	438.05	no data	no data
Nairobi	Kenya	II	117	high	920	5156.54	1766.15	2262.74	535.38	17.86	10.79
Ngorongoro Crater	Tanzania	VI	250	high	915	12399.42	2599.43	6187.65	3304.41	41.80	70.45
North Luangwa	Zambia	II	4636	medium	1028	1973.22	470.46	174.72	830.46	3.80	no data
Okavango	Botswana	II (partly)	20844	low	450	1317.29	145.03	86.67	780.58	1.28	0.21
Ruaha	Tanzania	II	42344	low	663	456.10	109.21	0.00	293.41	7.60	no data
Selous	Tanzania	IV	43626	medium	760	1725.97	67.26	129.62	1367.51	6.53	13.12
Serengeti	Tanzania	II	25000	high	855	8910.48	1302.01	6020.63	874.68	11.65	8.09
South Luangwa	Zambia	II	9050	medium	846	712.07	135.81	8.20	496.46	3.80	no data
Tarangire	Tanzania	II	2600	high	721	3972.31	547.61	1092.84	2120.12	no data	no data
Tsavo	Kenya	II	40572	low	553	353.79	69.01	0.00	199.33	1.02	no data

## Appendix 2.2: Species body weights

Species	Feeding type *	Region	female BW	pop BW	Source
Blue wildebeest	G	East Africa	163	122	Sachs,1967
Blue wildebeest	G	Southern Africa	180	135	Attwell,1982
Bohor reedbuck	G		41	31	Kingdon,1982
Buffalo	G	East Africa	576	432	Sinclair,1977
Buffalo	G	Southern Africa	513	385	Pienaar,1969
Bushbuck	BMF		33	25	Kingdon, 1982
Eland	BMF		300	225	Sachs,1967
Gemsbok/Oryx	G		210	158	Skinner & Smithers,1990
Gerenuk	BMF		31	23	Kingdon, 1982 (in Estes 1991)
Grant's gazelle	BMF		42	32	Sachs,1967
Greater kudu	BMF		157	118	Wilson, 1970
Hartebeest	G	East Africa	126	95	Sachs,1967
Hartebeest	G	Southern Africa	120	90	Smithers,1971
Impala	BMF	East Africa	42	32	Sachs,1967
Impala	BMF	Southern Africa	41	31	Smithers & Wilson,1979
Kob	G		63	47	Kingdon,1982
Lechwe	G		74	56	Skinner & Smithers,1990
Lesser kudu	BMF		58	44	Kingdon, 1982
Lichtenstein's hartebeest	G		166	125	Wilson,1966
Mountain reedbuck	G		29	21	Skinner,1980
Nyala	BMF		62	46	Tello & van Gelder, 1975
Oribi	BMF		14	11	Viljoen, 1982
Plains zebra	G	Southern Africa	322	241	Smuts,1975
Plains zebra	G	East Africa	219	164	Sachs,1967
Puku	G		61	46	Rosser,1987
Roan antelope	G		260	195	Kingdon,1982 (in Estes 1991)
Sable antelope	G		220	165	Kingdon,1982 (in Estes 1991)
Sitatunga	BMF		54	41	Kingdon, 1982
Southern reedbuck	G		38	29	Smithers & Wilson,1979
Springbok	BMF		37	28	Smithers,1971
Thomson's gazelle	BMF		16	12	Sachs,1967
Topi	G		109	81	Sachs,1967
Tsessebe	G		126	95	Child et al,1972
Warthog	BMF	East Africa	53	40	Sachs,1967
Warthog	BMF	Southern Africa	57	42	Mason, 1985
Waterbuck	G		175	132	Sachs,1967
Lion	C	East Africa	126	95	Pusey & Packer,1987 (in Estes 1991)
Lion	C	Southern Africa	126	95	Smuts,1982
Spotted hyena	C	East Africa	68	41	Kruuk, 1972
Spotted hyena	C	Southern Africa	55	51	Henschel, 1986

\* Feeding type: G = grazer; BMF = browser and mixed-feeder; C = carnivore

## **Chapter 3:**

# **Searching among zebras...** **The social behaviour and population dynamics of** **plains zebras: preliminary results from Hwange** **National Park, Zimbabwe**

Sophie Grange

Exploratory analysis



## **Abstract**

There is little information on the factors regulating or limiting African ungulate populations, particularly those of plains zebra. The demographic data currently available for large African herbivores are derived mainly from life tables but capture-mark-recapture (CMR) methods can provide accurate estimates of survival rates from individual-based studies. Using individual stripe patterns of plains zebra, I set up a study on the zebra population dynamics of Hwange National Park, Zimbabwe. The main objective of this study on a long-term basis is to obtain accurate survival estimates (age- and sex-specific). Field observations already provide data on the relative stability of family groups. Contrary to previous studies on the social structure of plains zebra, the family groups monitored in this park are quite unstable in composition with regard to their adult members. Adult females tend to switch more often between family groups, while yearling dispersal is relatively less important and probably delayed. The first estimates of annual survival rates are 78% for family stallions and 83% for adult females. The yearling (1-2 years old) survival is estimated to be around 70%. Foal survival (0-1 year old), which does not include neonatal mortality, was estimated at 89%. These preliminary estimates are not accurate, and more individuals with a greater number of recaptures are clearly necessary. However the estimate of adult female survival indicates that accounting for the structure in family groups is essential to obtain unbiased vital rates for this social species. The major bias in the juvenile survival estimate concerns the unknown neonatal mortality, and the percentage of foetus losses has to be estimated. To assess these two parameters, a reliable determination of the pregnancy status in adult mares is needed, notably through faecal samples.

The comparative analysis on wildebeest, buffalo and zebra populations in the Serengeti (see Chapter 1) highlighted the lack of demographic data on African ungulates – particularly for accurate vital rates. The Serengeti zebras presented a contrasted population dynamics compared to both grazing bovids, but to assess which demographic parameters are critical in this equid population we need to go further and estimate vital rates more accurately. This can be done on a long-term basis through capture-mark-recapture methods. Because of the large number of zebras (*c.a.* 150 000), it is not easy to launch such a study in the Serengeti ecosystem. In agreement with Hervé Fritz and Patrick Duncan, I therefore took the opportunity to start a monitoring program on the plains zebras in Hwange National Park, in collaboration with the HERD team, the CIRAD and Zimbabwean National Parks.

## **I - Introduction**

Plains zebras (*Equus quagga*) are present in most African ecosystems from the Southern Sudan and Ethiopia to Namibia and South Africa (Moehlman 2002). Many studies on plains zebras in East and South African ecosystems were done during the 1960's and 1970's. As medium-sized herbivores, plains zebras are also considered to be an important component of African mammal communities, and a good knowledge of their ecology and demography is therefore essential for the conservation and management of these equid populations.

The ecology and behaviour of zebras are well-known because of previous studies that mainly dealt with their particular social system, and also allowed comparisons between different populations and zebra species from East to South Africa (Klingel 1967, 1969a, Smuts 1976b, Monfort & Monfort 1978). Some studies were more focused on zebra demography, with a particular interest in reproduction (Klingel 1969b, Smuts 1976a). Shot samples of adult females have provided accurate data on female fecundity (Skoog & Gogan 1970, Smuts 1976a). Life tables have also been used, to estimate survival rates in several plains zebra populations (Skoog & Gogan 1970, Spinage 1972, Smuts 1976b, Monfort & Monfort 1978). However such estimates are known to be biased because this method assumes that the age structure of the sample reflects that of the live population, and because the assumption of a stable age structure in life tables is rarely met in natural populations. Recent studies have clearly shown the importance of age structure in the population dynamics of

long-lived species: it has notably been demonstrated that the age structure was not stable in several ungulate populations (Coulson *et al.* 2001; Clutton-Brock & Coulson 2002) and failing to account for differences between old and senescent individuals can over-estimate density-dependent effects on vital rates (Festa-Bianchet *et al.* 2003). Moreover life tables are generally built from dead samples. In the field, carcasses of juveniles disappear faster than those of adults, often leading to an under-representation of young age classes in the studied sample. Previous survival estimates for plains zebras were derived from life tables; there is therefore still a lack of accurate data on sex and age-specific survival rates for this species.

The development of capture-mark-recapture (CMR) methods for long-term studies has helped to improve the estimation of vital rates, particularly in Northern countries where wildlife management has been largely based on long-term studies and population models (Red deer: Catchpole *et al.* 2004; Soay sheep: Catchpole *et al.* 2000; Mountain goat and Bighorn Sheep: Festa-Bianchet *et al.* 2003; Roe deer: Gaillard *et al.* 1993). These studies can provide accurate demographic parameters. In Africa, the monitoring of African mammals has been mainly based on annual censuses. In the 1970's, shot samples provided data on vital rates for some ungulate species in particular ecosystems (especially the Serengeti and the Kruger National Park). However since then, for ethical and political reasons, many research programs no longer include animal shooting. Scientists preferentially monitor African wildlife populations through game counts and individual studies (generally with collared or tagged animals). These studies contribute more information on general ecology and behaviour (foraging, space use...), but also on population dynamics (Owen-Smith & Mason 2005; Owen-Smith *et al.* 2005). Individually-based studies applying CMR methods can provide reliable estimates of demographic parameters. The only study on an African ungulate using monitoring based on individual identification through natural marking is the Kudu population of the Kruger National Park, South Africa (Owen-Smith 1990). Because of subspecific and individual variations in their stripe pattern (Cabrera 1936) zebras can also be easily identified, which makes them ideal subjects for CMR studies. Petersen (1972) developed an identification system for zebra based on individual photos of family stallions in Nairobi National Park, and showed the efficiency of such a system for detailed studies of population dynamics or animal movements. Klingel (1967, 1969a) also used photo-identification to investigate the social structure and changes within family groups of plains zebra in the Ngorongoro Crater and the Serengeti National Park. However these studies did not investigate the population dynamics of plains zebra through the estimates of their vital rates.

In this chapter, I present the preliminary results of the first capture-mark-recapture study on the population dynamics of plains zebra in Africa. This project has been conducted in Hwange National Park, Zimbabwe. From July 2004, 50 identified individuals from 9 family groups were monitored every six months through a photo-identification technique. New zebras were identified and added to the database across fieldwork sessions. On a long-term basis the main objective of this CMR study is to obtain accurate survival rates for different sex and age classes in this population. During fieldwork, data on the dynamics of the social structure within different family groups have also been collected and are compared to previous studies on other plains zebra populations. Only one and a half years of monitoring is clearly not sufficient to obtain accurate estimates on survival rates. However, the first results are presented here and then discussed according to fieldwork observations and compared to the knowledge we already have on other zebra populations, both in terms of social system and demography.

## II - Material and Methods

### 1 - Study area

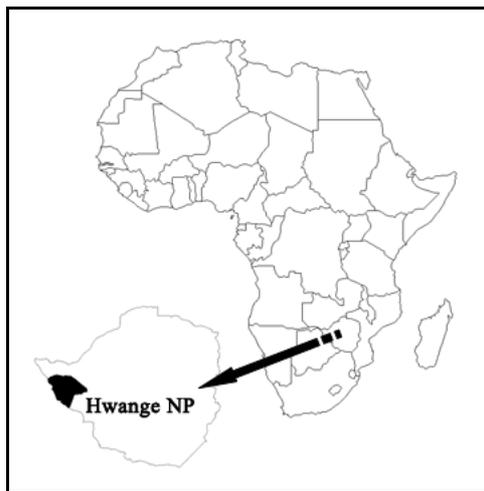


Figure 3.1. Hwange National Park (Zimbabwe)

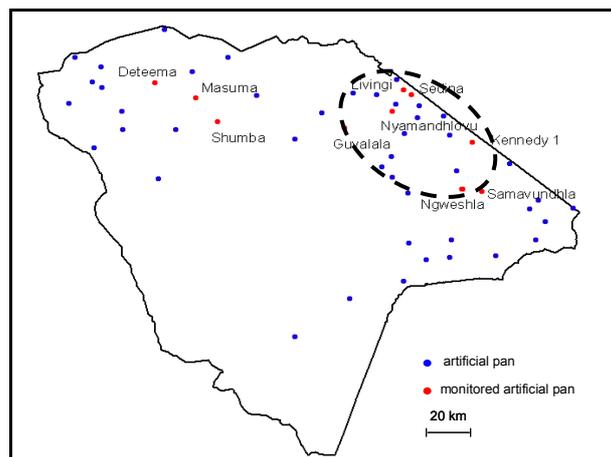


Figure 3.2. Study area in Hwange National Park (The black circle indicates the area prospected during fieldwork sessions)

The study was conducted in Hwange National Park (19°00' S, 26°30' E), which covers 14 651 km<sup>2</sup> in western Zimbabwe (Fig. 3.1). The annual rainfall averages 613 mm

(Chamaillé-Jammes *et al.*, in press). This ecosystem is characterized by the presence of artificial water points, which maintain relatively high densities of large mammals in the Northern part of the park, particularly during the dry season.

Plains zebras occurring in Zimbabwe belong to the same subspecies, *Equus quagga chapmani*. Their current distribution is primarily in Zimbabwe, with remnant populations occurring in north-eastern Botswana and southern Mozambique (Moehlman 2002). Observations on Hwange zebras started in July 2004, and fieldwork sessions were conducted every six months (January 2005, July 2005 and January 2006). All zebra families were identified and monitored in the Northern part of the park (Main Camp area; Fig 3.2), where water holes and an abandoned airstrip attract many grazers and provide a good visibility for observations. The zebra population of Hwange NP was estimated to be around 4000 individuals in 1973 and 3500 in 1989 (Wilson 1997). According to recent aerial censuses, this population declined significantly between 1990 and 1999 from 4193 to 2155 (population growth rate:  $r = -0.07$ ; linear model:  $n = 6$ ,  $p = 0.0054$ ,  $R^2 = 0.8820$ ; Fig. 3.3).

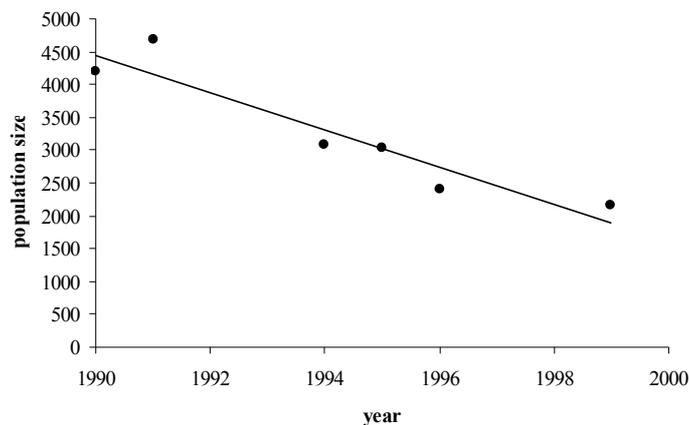


Figure 3.3. Zebra population sizes in Hwange National Park between 1990 and 1999

## 2 - Identification and monitoring

Zebras were identified individually from variations in stripe patterns. Special patterns like spots and irregular forks, but also the shoulder pattern, were very useful for identification (Klingel 1967). For each zebra, photos of both sides and the back were taken with a digital camera. These photos were then downloaded and used to complete and update individual sheets. The fieldwork was divided into several steps:

- 1- Selecting a family group: The selection implies that the family group can be clearly defined within a herd of zebras. After spending some time observing the interactions and movements of zebras, this was quite obviously the case. Zebras should also be easily approachable at a short distance to take good photos (it can take several days to follow and approach all members of the same family group without disturbing them during their daily activities).
- 2- Notes: Notes on the group composition (age and sex structure of the selected families) were taken, but also on individual body condition (visual index: 1 = poor, 5 = very good, adapted from Hennecke *et al.* 1981), predation marks (bite or claw marks, like breaks in the stripe pattern), pregnancy status (a pregnant mare is characterized by a very large belly because of a full womb, which is generally quite obvious from her profile) and mare-offspring links (the observation of suckling behaviour is used as a criterion to identify offspring's mares).
- 3- Identifying every family member: As the zebra stripe pattern is not symmetrical, zebras were identified one by one (*i.e.* until photos of both sides of the same individual have been taken).
- 4- Checking for known zebras: Every zebra seen in the field was compared visually to the photos of known zebras (thanks to a file containing all the individual sheets). Generally when a family group was seen, I tried to identify the stallion first, and then I checked adult mares. If the adult male was known, it was generally quicker to check for the other known members within the family group.

Zebra individuals were classified into three main age classes: adults, yearlings and foals. The two juvenile age classes were determined according to shoulder heights (Klingel, pers. comm.):

- Foal (0 – 12 months): the shoulder height is less than 75% of that of the mare.
- Yearling (12 – 24 months): the shoulder height is between 75% and 100% of that of the mare, but the body is thinner.

During the fieldwork some newborn foals were identified and aged with a precision of several days. Some individuals were also first identified as foals or yearlings and seen again as sub-adults, but there are then considered as adults in the population models.

The database was built in Microsoft ACCESS and included all sightings with individual characteristics (sex, age class, body condition, predation marks, and reproductive status), family structures, and individual photos. This database was updated over the course of the study: better photos of already known individuals were added, as were new individual sheets for new foals within known family groups. Some new families were also included. During one and a half years of study, 1316 individual sightings were recorded. In July 2004, 50 individuals were first identified within 9 family groups, and the sample size was increased through fieldwork sessions to reach 86 individuals in January 2006 (Table 3.1). Among zebras identified at each session, 70% were seen again in January 2005, 44% in July 2005, and 59% in January 2006.

Table 3.1. Sex and age structure of identified zebras between July 2004 and January 2006  
(The age classes indicated here are the ones at first capture)

		July 2004		January 2005		July 2005		January 2006	
		prev.	new	prev.	new	prev.	new	prev.	new
Adult	Male	0	11	11	3	14	1	15	1
	Female	0	24	24	5	29	5	34	4
Yearling	Male	0	7	7	0	7	1	8	0
	Female	0	2	2	0	2	1	3	0
Foal	Male	0	2	2	5	7	0	7	2
	Female	0	3	3	0	3	2	5	5
	Unknown	0	1	1	0	1	0	1	1
<i>Total</i>		<i>0</i>	<i>50</i>	<i>50</i>	<i>13</i>	<i>63</i>	<i>11</i>	<i>74</i>	<i>12</i>

\* prev. = previously identified individuals; new = new identified individuals

### 3 - Statistical analysis

Variations in family group sizes across the four fieldwork sessions were tested with ANOVAs (when variables were normally distributed and the homogeneity of variances was verified). Variations in age structure, foal/mare and juvenile/mare ratios across periods were tested with a G-test of independence ( $\chi^2$ ). Statistical tests were performed with R-software (version 2.0.1., 2004).

The stability of family groups was measured through changes in the composition of family members. The “stability” itself concerns adult members and was compared to those obtained during the study on Ngorongoro zebras (Klingel 1967, 1969a) using a G-test of independence (with Yale’s continuity correction). Changes within family groups including stallions, adult mares or sub-adults were also described.

Population models were performed with M-SURGE software (Choquet *et al.* 2005a) and I used the same notation as Lebreton *et al.* (1992): where  $\Phi$  is the survival probability,  $t$  the time period (in this study, the time interval is 6 months),  $p$  the capture probability,  $s$  the sex and  $g$  the group (here, it refers to “family group”). Before implementing the data in M-SURGE, goodness-of-fit (GOF) tests were performed using U-CARE software (Choquet *et al.* 2005b). This program tests for the homogeneity of recapture probabilities independent of capture order, and looks for possible differences in recapture probabilities independent of survival. The tests do not indicate problems in the global data files of adult males, adult females, and foals (Appendix 3.1). When family groups were considered for adult females, yearlings and foals, GOF tests could not be performed because of the lack of data, but this does not prevent an exploratory analysis.

We estimated survival of adult males and females separately because of the harem structure (the probability of seeing a family stallion is linked to those of seeing its associated adult mares). M-SURGE models for adult males (here, family stallions) therefore include time-dependence on survival and/or capture probability. In CMR models, the assumption of the independence of individuals has to be respected. Consequently models performed on adult females, yearlings and foals consider individuals within different family groups: both effects of time and family group are therefore tested in these cases. As there is no marked dimorphism in plains zebra during the first years of age (Smuts 1975) and as both sexes dispersed, there is no biological evidence for high sex differences in the estimates of yearlings or foals. Both sexes are therefore pooled in the models of these two young age classes.

The most parsimonious model was selected according to the Akaike Information Criterion (AIC): the selected models are those with the lowest AIC (Burnham and Anderson 1992). When models differ in AIC by less than two units, the simplest model is selected (Burnham and Anderson 1998).

### **III – Preliminary results**

#### *I – Changes within family groups*

The mean family group size did not vary during the study period (ANOVA:  $F_{3,30} = 0.5169$ ,  $p = 0.6738$ ), and averaged 5.3 individuals (Fig. 3.4).

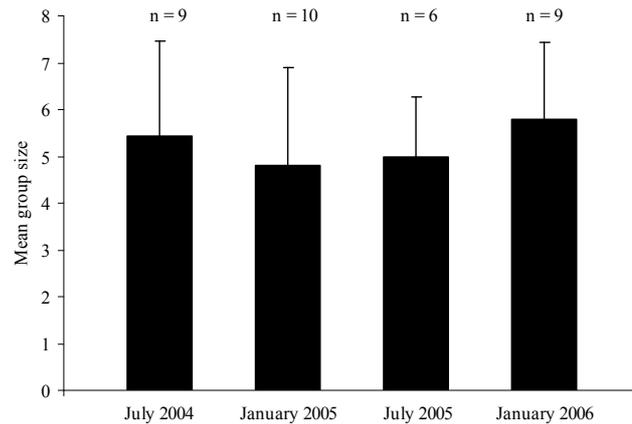


Figure 3.4. Variations in family group size

The age structure was also very stable across periods (Fig. 3.5) with no significant variation in the proportions of adult and sub-adult, yearlings and foals ( $\chi^2_{(6 \text{ df})} = 3.5586$ ,  $p = 0.7362$ ). On average the zebra family groups were composed of 73% adults and sub-adults, 17% yearlings, and 10% foals.

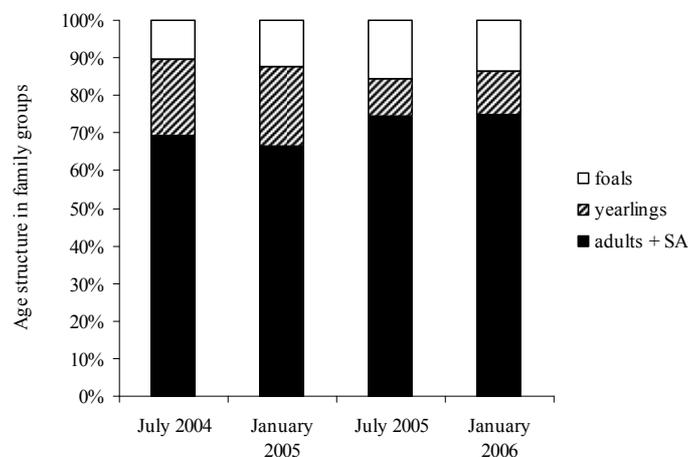


Figure 3.5. Variations in the age structure of family groups

The annual stability of family groups was significantly lower in Hwange (2 out of 12 families, *i.e.* 17%) compared to Ngorongoro Crater (8 out of 11 families, *i.e.* 73%): G-test:  $\chi^2 = 5.2356$ ,  $df = 1$ ,  $p = 0.0221$  (Appendix 3.2). However family stallions disappeared in 4 out of the 12 studied families in Hwange (33%), and only 2 out of the 11 families of Ngorongoro (18%). The incorporation of adult mares in new family groups seems to be more frequent in Hwange (5 out of 12 families, *i.e.* 42%) compared to Ngorongoro Crater (1 out of 11 families,

*i.e.* 9%). There were also fewer departures by young mares in Hwange (2 out of 12 families, *i.e.* 17%) compared to Ngorongoro Crater (4 out of 11 families, *i.e.* 36%).

### 2 - Reproduction

Among 24 adult mares identified in July 2004, 16 were followed for more than 6 months after their first “capture”. 75% of these mares had foals during our study period. 9 mares were well followed between re-capture sessions (*i.e.* first captured in July 2004 and seen again in January 2006). The age of yearlings and foals was therefore evaluated visually (see Methods), and from personal observations it is possible to obtain a rough estimate of the dates of birth: 1 mare had 2 foals in 2.5 years (0.80 foal/mare), 7 had on average 2 foals in 3.5 years (0.67 foal/year), and 1 had no foal during the study period (0 foal/year). The mean foaling rate is therefore 0.61 foal/mare/year.

In the known family groups, the foal/mare ratio does not vary significantly across study periods ( $\chi^2_{(3 \text{ df})} = 0.7913$ ,  $p = 0.8516$ ), and averages 0.28. When we consider all offspring (foals and yearlings), the juvenile/mare ratio also appears relatively stable between periods ( $\chi^2_{(3 \text{ df})} = 0.9665$ ,  $p = 0.8118$ ), with a mean value of 0.61.

### 3 - Survival rates

Survival was estimated for adult males ( $n = 15$ ), adult females ( $n = 34$ ), yearlings ( $n = 11$ ) and foals ( $n = 12$ ). Models are indicated in Tables 3.3.

Two models can be selected for adult males ( $\Delta \text{AIC} < 2$ ). The first one is the constant model and the second one includes time-dependence of the capture probability (Table 3.3a). In the second model, the capture probability averages 0.78 (95% CI: 0.56-0.93). This mean value is within the confidence limits of the constant model estimate: 0.71 (95% CI: 0.45-0.88). The simplest model “ $\Phi p$ ” is selected in this case (as recommended by Burnham and Anderson 1998) which leads to an adult male survival constant across our study period, with an annual estimate of 0.78 (95% CI: 0.43-0.94).

Table 3.3. Population models  
(The selected models are shown in bold)

Table 3.3a – Adult males

Model	n	Deviance	AIC
<b><math>\Phi</math> p</b>	<b>2</b>	<b>52.484</b>	<b>56.484</b>
$\Phi$ p <sub>t</sub>	4	49.816	57.816
$\Phi$ <sub>t</sub> p	4	50.75	58.75
$\Phi$ <sub>t</sub> p <sub>t</sub>	5	49.382	59.382

Table 3.3b – Adult females

Model	n	Deviance	AIC
<b><math>\Phi</math> p<sub>t+g</sub></b>	<b>16</b>	<b>64.012</b>	<b>96.012</b>
$\Phi$ <sub>t</sub> p <sub>t+g</sub>	18	63.8087	99.8087
$\Phi$ p <sub>t</sub>	4	92.8856	100.8856
$\Phi$ <sub>t</sub> p <sub>t</sub>	5	91.6063	101.6063
$\Phi$ <sub>t</sub> p	4	93.9192	101.9192
$\Phi$ p <sub>g</sub>	14	74.7769	102.7769
$\Phi$ p	2	99.0066	103.0066
$\Phi$ <sub>txg</sub> p <sub>txg</sub>	36	32.2246	104.2246
$\Phi$ <sub>g</sub> p <sub>t</sub>	16	73.0517	105.0517
$\Phi$ <sub>g</sub> p	14	77.3708	105.3708
$\Phi$ <sub>g</sub> p <sub>g</sub>	21	64.2217	106.2217
$\Phi$ <sub>g</sub> p <sub>t+g</sub>	26	54.2494	106.2494
$\Phi$ <sub>t+g</sub> p	16	74.6991	106.6991
$\Phi$ <sub>t</sub> p <sub>g</sub>	16	74.7491	106.7491
$\Phi$ <sub>t+g</sub> p <sub>t</sub>	18	72.6786	108.6786
$\Phi$ <sub>t</sub> p <sub>txg</sub>	33	43.1468	109.1468
$\Phi$ <sub>t+g</sub> p <sub>t+g</sub>	28	53.6354	109.6354
$\Phi$ <sub>g</sub> p <sub>txg</sub>	36	38.0973	110.0973
$\Phi$ p <sub>txg</sub>	32	47.0982	111.0982
$\Phi$ <sub>t+g</sub> p <sub>g</sub>	26	59.7518	111.7518
$\Phi$ <sub>t+g</sub> p <sub>txg</sub>	36	39.8627	111.8627
$\Phi$ <sub>txg</sub> p <sub>t+g</sub>	36	39.8627	111.8627
$\Phi$ <sub>txg</sub> p <sub>g</sub>	36	48.8469	120.8469
$\Phi$ <sub>txg</sub> p <sub>t</sub>	33	57.9713	123.9713
$\Phi$ <sub>txg</sub> p	32	63.5602	127.5602

Table 3.3c – Yearlings

Model	n	Deviance	AIC
$\Phi$ <sub>t</sub> p <sub>t</sub>	5	21.868	31.868
$\Phi$ <sub>t</sub> p	4	24.4345	32.4345
<b><math>\Phi</math> p</b>	<b>2</b>	<b>29.1162</b>	<b>33.1162</b>
$\Phi$ p <sub>t</sub>	4	27.4489	35.4489
$\Phi$ <sub>t+g</sub> p <sub>t</sub>	14	12.3073	40.3073
$\Phi$ <sub>g</sub> p	10	20.5083	40.5083
$\Phi$ <sub>t+g</sub> p	12	17.102	41.102
$\Phi$ <sub>g</sub> p <sub>t</sub>	12	18.6582	42.6582
$\Phi$ <sub>t</sub> p <sub>t+g</sub>	14	15.1379	43.1379
$\Phi$ p <sub>g</sub>	10	23.5941	43.5941
$\Phi$ <sub>g</sub> p <sub>g</sub>	14	16.6355	44.6355
$\Phi$ <sub>t</sub> p <sub>g</sub>	12	20.6831	44.6831
$\Phi$ p <sub>t+g</sub>	12	21.6269	45.6269
$\Phi$ <sub>txg</sub> p <sub>txg</sub>	22	2.7726	46.7726
$\Phi$ <sub>txg</sub> p <sub>t+g</sub>	22	2.7726	46.7726
$\Phi$ <sub>t+g</sub> p <sub>t+g</sub>	21	5.5452	47.5452
$\Phi$ <sub>g</sub> p <sub>txg</sub>	22	4.4987	48.4987
$\Phi$ <sub>txg</sub> p <sub>g</sub>	22	6.5917	50.5917
$\Phi$ <sub>g</sub> p <sub>t+g</sub>	19	12.8164	50.8164
$\Phi$ <sub>t+g</sub> p <sub>g</sub>	19	13.2945	51.2945
$\Phi$ <sub>t</sub> p <sub>txg</sub>	22	8.1793	52.1793
$\Phi$ p <sub>txg</sub>	22	8.3178	52.3178
$\Phi$ <sub>t+g</sub> p <sub>txg</sub>	22	8.3178	52.3178
$\Phi$ <sub>txg</sub> p <sub>t</sub>	22	8.8009	52.8009
$\Phi$ <sub>txg</sub> p	22	10.7129	54.7129

Table 3.3d – Foals

Model	n	Deviance	AIC
<b><math>\Phi</math> p<sub>t+g</sub></b>	<b>11</b>	<b>13.2693</b>	<b>35.2693</b>
$\Phi$ <sub>t</sub> p <sub>t+g</sub>	13	11.2868	37.2868
$\Phi$ p <sub>t</sub>	4	29.5478	37.5478
$\Phi$ <sub>txg</sub> p <sub>txg</sub>	16	6.5917	38.5917
$\Phi$ <sub>txg</sub> p <sub>t+g</sub>	16	6.5917	38.5917
$\Phi$ <sub>t+g</sub> p <sub>t+g</sub>	16	6.5917	38.5917
$\Phi$ p	2	34.7035	38.7035
$\Phi$ <sub>g</sub> p <sub>t</sub>	11	17.2794	39.2794
$\Phi$ <sub>t+g</sub> p <sub>t</sub>	13	13.3798	39.3798
$\Phi$ <sub>t</sub> p <sub>t</sub>	5	29.5062	39.5062
$\Phi$ p <sub>g</sub>	9	22.6613	40.6613
$\Phi$ <sub>g</sub> p <sub>t+g</sub>	15	10.7105	40.7105
$\Phi$ <sub>t</sub> p <sub>txg</sub>	15	11.2868	41.2868
$\Phi$ <sub>t</sub> p	4	33.4474	41.4474
$\Phi$ <sub>t</sub> p <sub>g</sub>	11	20.5532	42.5532
$\Phi$ <sub>g</sub> p <sub>txg</sub>	16	10.7105	42.7105
$\Phi$ p <sub>txg</sub>	15	13.1833	43.1833
$\Phi$ <sub>txg</sub> p <sub>t</sub>	15	13.3798	43.3798
$\Phi$ <sub>g</sub> p	9	25.5281	43.5281
$\Phi$ <sub>g</sub> p <sub>g</sub>	12	19.8913	43.8913
$\Phi$ <sub>t+g</sub> p <sub>g</sub>	15	14.9094	44.9094
$\Phi$ <sub>t+g</sub> p <sub>txg</sub>	16	13.1833	45.1833
$\Phi$ <sub>txg</sub> p <sub>g</sub>	16	14.9094	46.9094
$\Phi$ <sub>t+g</sub> p	11	25.7819	47.7819
$\Phi$ <sub>txg</sub> p	15	20.2892	50.2892

For adult females, the model “ $\Phi p_{t+g}$ ” is the one with the lowest AIC ( $\Delta AIC > 2$  compared to the second best model; Table 3.3b). It indicates that survival is constant and the capture probability appears to vary according to the time period and the family group (13 groups). The annual female survival is therefore estimated to be 0.83 (95% CI: 0.62-0.93). The capture probability varies in time: 0.70 (95% CI: 0.15-0.95) for the first recapture, 0.09 (95% CI: 0.01-0.64) for the second one, and 0.46 (95% CI: 0.06-0.89) for the third one. The model estimates the capture probability well in 7 family groups out of 13: the mean values vary from 0.19 (95% CI: 0.02-0.68) to 0.67 (95% CI: 0.14-0.97).

There is no effect of the family group on the survival and the capture probability of yearlings. Three models can be selected (Table 3.3c). In the first model (“ $\Phi_t p_t$ ”), survival cannot be well estimated for the third period and the capture probability is only estimated for the first period. In the second model (“ $\Phi_t p$ ”), yearling survival cannot be estimated for the third period. As recommended by Burnham and Anderson (1998), the simplest one is selected here (“ $\Phi p$ ”). The annual yearling survival is estimated around 0.70 (95% CI: 0.42-0.89) and the capture probability around 0.94 (95% CI: 0.64-0.99).

For foals, the model “ $\Phi p_{t+g}$ ” is selected (Table 3.3d). The annual survival estimate is therefore constant and around 0.89 (95% CI: 0.51-0.99). The capture probability varies according to the time period and the family group, and can be estimated for only 2 family groups out of 8: 0.50 (95% CI: 0.06-0.94) for group 1 at the second recapture, and 0.56 ((95% CI: 0.05-0.97) for group 5 at the third capture. For 12 foals followed during this study, I was able to follow the mares at least until the foals potentially reached the yearling age class. In 3 cases, the mare was seen without her foal. As young zebras do not generally disperse before 2-years-old and as there is no adoption in plains zebra, these foals were probably dead (25% of known foals).

#### 4 - Modelling

Using the estimates obtained here, I built a population model based on a Leslie matrix. This pre-breeding model is female-based and age-structured: it therefore includes the survival estimates of adult females (0.83), yearlings (0.70), foals (0.89), and the female fecundity (foaling rate = 0.61 foal/mare/year). According to previous studies, the age at first

reproduction is fixed at 3 years old and the sex-ratio at birth is 0.50 (for example, see the Serengeti zebra model in Grange *et al.* 2004).

After simulations with ULM software, the model predicts a slight annual decrease of 1% in this population ( $\lambda = 0.99$ ). This figure is in agreement with the last estimates of the zebra population size in Hwange (2393 zebras in 1996 and 2155 in 1999, indicating 3% of decrease). The mean generation length is 8.17 years.

#### **IV - Discussion**

This study of zebra population dynamics is the first one using a capture-mark-recapture method to estimate sex and age-specific survival rates in an African ungulate. Even though the study period is still too short to obtain accurate demographic parameters (the monitoring only started in July 2004), field observations already provide interesting results.

The social system of plains zebra has been well studied (Klingel 1967, 1969a, Smuts 1976b, Monfort & Monfort 1978). In Hwange, the family groups averaged 5.3 individuals; which is close to the previous estimate for this park (4.6 individuals, in Klingel 1967, 1969a). The mean sizes of zebra family groups in Etosha, Kruger and Serengeti were also close to 5 individuals; in Ngorongoro the group size was a little higher (Klingel 1967, 1969a).

The main finding of the previous studies on plains zebra was that family groups (or harems) are very stable in the adult age class. In Ngorongoro Crater, Klingel (1967) found that more than 70% of family groups were stable during one year of monitoring (Appendix 3.2). In Kruger National Park (South Africa), Smuts (1976b) reported a very high stability in harem composition: the family groups that were collar-marked and identified remained unchanged, except for the addition of mares or the birth and death of foals. In this study, only 17% of the monitored families stayed stable during one year. During the year and a half of zebra monitoring in Hwange, family groups disappeared or were broken up 5 times: in one case the whole family group was not seen again; in 3 cases the family stallion disappeared but some mares were seen in other family groups; and in the last case another male acquired the whole family of the known stallion. One hypothesis to explain the dislocation of family groups is that the death of the stallion induces the dispersal of all family members if another stallion does not take over the family group. In Ngorongoro, Klingel (1967) observed that of 5

family stallions that disappeared, 3 of them died and the other 2 were old males that were replaced by another stallion and then joined bachelor groups.

Some other changes within family groups tend to occur more or less often in this study compared to the previous observations in Ngorongoro. In the Hwange population there was apparently a quite high rate of changes in adult females between families compared to Klingel's study. This observation certainly results from the lower stability of family groups, which could be explained by the inability of stallions to maintain permanently their harems (because of a high competition between males or perturbations that increase visual loss or distance between family members), or by a high turn-over in the adult population (*i.e.* a relatively high mortality in adults). There is no evidence that diseases seriously affected the Hwange zebra population and field observations showed that all adults were in very good body condition during the year, except some adults badly hurt after a lion predation attempt. There was also no visual sign of high parasitism. In this population therefore, most adult zebra mortality is probably due to predation, and to a lesser extent to poaching which occurs sometimes in the park (we removed a snare on one adult mare in July 2005).

Moreover I observed only few departures of young males and females from their family groups. Of the 9 young zebras (foals and yearlings) followed during this study and seen again when they reached the sub-adult age class, only 33% had dispersed (2 females and 1 male). This observation suggests that in this population young zebras tend to disperse preferentially after 24 months of age, but more fieldwork sessions are necessary to confirm this trend and to estimate the age at dispersal. Klingel (1969a) observed that the main factor causing dispersal of young mares was their abduction by another stallion. In Hwange, it is probably because of the adult mare behaviour and the loss of bonds due to the arrival of a new foal. One mare clearly showed an aggressive behaviour towards her yearling when it tried to approach her newborn foal. One week later the yearling had left her family group.

The observations on mares provided few data on their reproduction: most adult females reproduced during the study period and they tended to foal twice every three years. This result is based on visual estimates of the age of offspring, but the number of foals of precisely known age should increase in future years, allowing a more accurate estimation of the foaling rate for this population. However these results are in agreement with the Ngorongoro study where 15% of adult mares had 3 foals in 3 years, 33% had 2 foals, 42% had 1 foal, and 10% had no offspring (Klingel 1969b), leading to a foaling rate of 0.51 foal / mare / year (estimate based on surviving foals). In Hwange, the annual foaling rate averages

0.61 foal / mare / year. The foal/mare ratio was quite stable across fieldwork sessions, suggesting that foaling could occur all along the year. However, the shoulder height of known foals and observations of newborns indicate that births probably occur preferentially during the rainy season (December – April), and particularly at the beginning of this season. In Ngorongoro, 80% of foals were born in the rainy season and there was apparently a relation between the foaling rate and the total amount of rainfall during the previous year in several parks including Hwange in 1965 (Klingel 1969b).

The estimation of the pregnancy status of adult mares was done visually in the field, but this method is not accurate, particularly to detect early gestation. A collect of female faecal samples will be done regularly in future. The concentration of progesterone generally gives good information on pregnancy status and has been tested on other equid populations (Asa *et al.* 2001).

The first population models presented here are only preliminary as the study period is quite short. However, adult survival was estimated during this study, with 78% for family stallions and around 83% for mares (> 2 years-old). The confidence intervals are too large to highlight any significant difference between sexes, and more data are needed to increase the precision of these estimates. The first estimates obtained for plains zebra in Hwange are similar to those derived from life tables in other populations. The zebra adult survival in Akagera reached 89% for young adults (2 to 9 years-old) and 70% for senescent individuals (> 9 years-old), and averaged 78% for the whole adult age class (Monfort & Monfort 1978). In Kruger National Park, zebra female survival was 93 and 91% for 2-9 year-olds and 77 and 74% for senescent mares, respectively estimated from the life tables of Spinage (1972) and Smuts (1976b). On average, Kruger female survival after two years of age was between 81 and 83%. The estimate of adult female survival in Hwange (83%) is therefore in agreement with previous estimates from other populations when the survival rates of prime-age and senescent females are combined.

The capture probability of adult females depends on both time and family group. According to the harem structure in plains zebra, this result is not surprising because if mares are more or less permanently associated within family groups they should present similar capture probabilities. Failing to account for the variability among family groups in capture probability would have given severely biased estimates. From the “ $\Phi$  p” model the average survival of adult females is estimated to 0.64, whereas the unbiased estimate is 0.83. This modelling exercise clearly demonstrates that the social structure has to be considered

carefully in studies on population dynamics, particularly when survival has to be estimated from a capture-mark-recapture method. Consequently in species with particular social systems leading to long-term associations between individuals – such as family groups (most wild equid species: Klingel 1974), prides (lions: Schaller 1972) or a strongly structured matriarchy (elephant: Douglas-Hamilton 1972) – the “group” effect has to be considered in CMR models to avoid biases in survival estimates. Such biases could therefore appear in all species where associations between individuals occur at least permanently during a biological period (*e.g.* reproductive season), which includes ungulates with females gathered in leks (*e.g.* topis) and every kind of association between sexes (*e.g.* the groups of females and their offspring in impalas).

The effect of time on the capture probabilities of adult females is in agreement with observations across fieldwork sessions: the highest proportion of recaptures occurs in January 2005 (first occasion of recapture: 70%) and the lowest in July 2005 (second occasion of recapture: 44%). In dry season (sessions in July), the visibility is increased, but zebra herds are more dispersed in the park (probably looking for shade in less open habitats): zebra groups are therefore mainly “recaptured” around pumped water holes during the day. In wet season (sessions in January) many zebra groups are concentrated on the airstrip where they can find short and green grasses: they are easier to “recapture” as they remain in open habitats during a large part of the day. These preliminary observations suggest a difference in spatial use by Hwange zebras between dry and wet seasons, but more data are needed to confirm this trend.

The modelling for yearlings included 11 individuals. Previous estimates of survival based on life-tables were very variable (respectively 0.52, 0.79 and 0.92 in Smuts 1976b, Monfort & Monfort 1978, and Spinage 1972). The annual yearling survival in Hwange is estimated at around 70%, which seems to be correct. The main problem is that the capture probability is over-estimated (94%) compared to field observations. Because of dispersal at yearling age we should expect a lower capture probability, but it is probable that in the Hwange population juveniles mainly disperse after reaching 2 years of age. Three yearlings have been “recaptured” after dispersal to other groups (family or bachelor groups). Field observations are not in agreement with the very high estimate of capture probability (94%), perhaps because the selected model leads to biased estimates. As yearling dispersal can also bias survival, it is necessary to make more observations on bachelor groups and unknown family groups to increase the probability of “recapture” for known yearlings that have dispersed.

The estimate of foal survival (one year-old) is only based on 12 individuals, and there is also a lack of precision with large confidence intervals. More data is clearly needed to obtain accurate survival estimates. In Hwange, the survival of foals is estimated to be 89%, but this value does not include neonatal mortality. In July, foals were first identified several months after birth (age estimate = 3-6 months). It was easier to age foals in January, and regular observations led to accurate estimates of the date of birth (to within a few days). The foal survival estimate obtained for this population cannot therefore include foal mortality occurring in the first days (or sometimes weeks) after birth. In Ngorongoro, of 158 foals followed during their first year of life, only 5% disappeared (Klingel 1969a), indicating a relatively high post-natal survival (95%). Previous studies in the Serengeti and Kruger National Park gave foal survival estimates around 40% (Grange *et al.* 2004; Mills & Shenk 1992), which suggests that neonatal mortality should be quite important in plains zebras. When the pregnancy status of adult mares has been assessed through faecal samples, I should be able to estimate the neonatal mortality in the Hwange zebra population. From field observations, I can assume that 75% of known foals survive during their first year (neonatal mortality not included), which seems to be in agreement with the model estimate, but more data are needed. The capture probability of foals depends on time and family group. As foals are associated with their mares we can expect to find similar effects on their capture probabilities. However in foals, these probabilities can only be estimated for 2 groups and averaged 53%.

The estimates of survival and fecundity obtained in this study should not be very biased as they led to a realistic (although simple) population model suggesting a slight annual decline in this zebra population ( $\lambda = 0.99$ ). Moreover the mean generation length obtained with this matrix model (8.17 years) is close to the one obtained for the Serengeti zebra population (8.24 years, in Grange *et al.* 2004); and in both cases the plains zebra populations remain relatively stable. During the last decade, game counts highlighted a decline of 7% in the Hwange zebra population, such a difference compared to the model may indicate that the studied sample is not representative of the Hwange population. The number of identified zebras during this study effectively represents about 3% of the total zebra population in Hwange National Park. However, the capture probabilities are quite high, reflecting a relative fidelity of the monitored family groups to the area prospected. It is therefore quite probable that most of these zebras belong to a sub-population, and that the family groups recaptured during all fieldwork sessions are resident around the Main Camp area (Fig. 3.2). Among these

groups, several were first identified around different water holes, and generally join the family groups first identified on the airstrip (open area in Main Camp) during the rainy season, leading to high zebra concentrations in this particular area, which facilitates the number of recaptures. One out of the 3 family groups first identified around Dopu water hole in July 2004 has not been recaptured since January 2005. As the family members have not been seen within other groups, it could indicate that the whole family group has left the study area. In the Serengeti ecosystem (25000 km<sup>2</sup>), zebra migration occurs every year. Some family groups are migratory and other ones are resident. Hwange is a large National Park (15000 km<sup>2</sup>), and it is therefore possible that some family groups are more or less resident within particular areas. To answer this question, data on zebra movements (*e.g.* with GPS collars) would be needed. In the Serengeti, it has been suggested that predation can limit the zebra population, notably through its potential impact on juvenile survival (Grange *et al.* 2004). Compared to the Serengeti study, the estimate of foal survival obtained here is quite high (89%). However in Hwange National Park, predator densities are not very high (0.02 and 0.06 individuals/km<sup>2</sup> for lions and hyenas respectively), compared to the Serengeti ecosystem (0.12 and 0.20 individuals/km<sup>2</sup>). If Hwange zebras are effectively divided into sub-populations, it could be therefore interesting to select another study area (around Masuma and Deteema, in the eastern part of Hwange) where the predator densities are higher than around Main Camp.

This first study has provided information on both the stability of family groups and the population dynamics of Hwange zebras. Although the sample size is not very large and will be increased in future years (Box 3.1), this study provides adequate data to estimate sex and age-specific survival rates through a CMR method. This is thanks to two factors that maximise the power of CMR calculations by increasing the number of “recaptured” animals through time (*i.e.* a greater number of “1” in individual life histories). First, the estimates of capture probability are generally high (>50%) and secondly, the plains zebra is a long-lived species. The main result regarding social structure was that family groups are less stable compared to other studies. Because of such instability, changes of adult females between families are quite common compared to other zebra populations. The estimates of survival and fecundity obtained in this study appear to be biologically realistic. One interesting result is the first estimate of foal survival based on a capture-mark-recapture model. To improve the accuracy of this estimate, I need to increase the sample size and take into account the neonatal mortality through the assessment of the reproductive status of mares in the field. The other major result highlighted by this modelling exercise is that to obtain unbiased estimates of

survival, it is important to account for the species' social structure in population models. Finally, these preliminary results show that a CMR method based on individual stripe pattern can be easily applied to study the population dynamics of plains zebra.

### **Acknowledgements**

I would really like to thank the CIRAD Zimbabwe & the National Parks, as well as Hervé Fritz and Patrick Duncan, for giving me the opportunity to work on zebras in Hwange National Park. This study was funded by the PICS France / South Africa (n° 1452). Patrick Duncan provided a car and a digital camera, and also helped during the last fieldwork session. Many thanks also to Marion Valeix who kindly accepted me as a member of her “Hwange dream team”. Marion Valeix and Simon Chamaille-Jammes also provided maps of Hwange National Park. I would like to thank Jean-Michel Gaillard for his precious help with the modelling, but also Ségolène Dubois, Géraldine Fleurance, and Alison Duncan for their help during fieldwork sessions. Finally I would not be able to do my fieldwork without Owen Mangwana, whose mechanical skills proved to be very efficient and vital for the “zebra project”. I am also grateful to the zebras for their kind cooperation during the fieldwork!

#### **Box 3.1 – A computer program for zebra identification**

One of the next steps of this study is to increase the current sample size of individuals identified in this population. The major problem is that a large sample necessitates more time to be able to recognize known individuals. It is quite difficult for another observer to recognize zebras that I have already identified, but this problem is solved after some fieldwork when known family groups have been followed for several days.

To improve and facilitate the individual recognition, we plan to use a computer program. It is therefore essential to get the best photos of zebra profiles (perfect alignment of the body, no shades on the stripes, and high digital quality). Tilo Burghardt (University of Bristol) is currently building the program with these photos: the system is based on variations in individual stripe pattern, exactly like with finger prints. This program will allow us to increase considerably our sample size (which is essential to obtain accurate estimates), it could be easily used by different observers, and it will make individual recognition far more efficient in the field.

### Appendix 3.1 – Goodness of fit tests with U-CARE

(The number of different groups considered is indicated in numbers for “sex” and “family”; and the term “All” is used when different groups were pooled into one. “NA” indicated that tests cannot be performed)

Class	Sex	Family	Global test			Transient		Trap dependence	
			Chi <sup>2</sup>	p	Statistic	p (2 sided)	p (1 sided)	Statistic	p
Adult male (n = 15)	1	All	1.4513 (4 df)	0.8352	-0.5051	0.6135	0.6933	0.6745	0.5
Adult female (n =34)	1	All	1.5987 (4 df)	0.8090	-0.7860	0.4319	0.7841	0	1
Adult female (n =34)	1	13	NA	NA	NA	NA	NA	NA	NA
Yearling (n = 11)	All	All	NA	NA	NA	NA	NA	NA	NA
Foal (n = 12)	All	All	0.9359 (3 df)	0.8168	0.6841	0.4939	0.2470	NA	NA
Foal (n = 12)	2	All	0.9359 (3 df)	0.6263	0.6841	0.4939	0.7530	NA	NA
Foal (n = 12)	All	8	NA	NA	NA	NA	NA	NA	NA

### Appendix 3.2 – Changes within family groups between this study (12 families followed during one year) and Klingel’s study (11 families followed during one year).

	Hwange	Ngorongoro
<i>studied families</i>	12	11
stable family groups (adults unchanged)	2	8
families where stallion disappeared	4	2
families where adult mares disappeared	3	2
families with adult mares incorporated	5	1
families with young mares taken into family	2	1
families with young mares departed from family	2	4
families with young stallions disappeared	3	4

## **Chapter 4:**

# **Is the feralization of domestic horses a sexist process?**

Sophie Grange, Patrick Duncan, Michel-Antoine Leblanc and Jean-Michel Gaillard

Paper in preparation



## Abstract

When animals return to the wild they experience a process called “feralization”. Previous studies on “feral” animals showed that these populations generally present different patterns and variations in terms of social behaviour, which induce changes in sex ratio. This suggests that during feralization animals should exhibit differences in terms of population dynamics. However, such changes in demographic parameters have never been investigated precisely and nothing is known about the impact of feralization on the population dynamics of domestic herbivores. We study the consequences of feralization on the demography of Camargue horses. This population rapidly reached its food ceiling, which provided a perfect experiment to test the effects of feralization during a strong increase of density. The results show that adult females are more sensitive to density than males are, and that their survival strongly depends on food resources. These differences in adult mortality between males and females lead progressively to a male-biased sex ratio. Model simulations predict that this population would reach a threshold (*c.a.* 160 horses) and experience a strong decrease in its growth rate with a low foal/mare ratio and a higher proportion of adults. Interestingly the survival of young horses reacts later than expected by Eberhardt’s model: this could be due to the high investment of mares in reproduction. Camargue horses returned rapidly to a “wild” social organization based on a harem structure, and comparisons with other wild horses show that the effects of density-dependence after release do not necessarily induce “natural” dynamics. Fertility controls or the manipulation of sex ratios could therefore be useful in this case to restore a population dynamics similar to those of wild equids in natural ecosystems.

**Keywords:** Conservation, feralization, equids, population dynamics, sex ratio

## I - Introduction

Since the 1980's – particularly in Europe and the United States – the management of mammal communities has represented a major challenge for the conservation and preservation of natural ecosystems. Through their fundamental effects on plant succession, mammalian herbivores, particularly large grazers, are indeed considered as keystone species in many ecosystems (Danell *et al.* 2006). Another important challenging question is to restore “natural systems” through wild animal reintroductions (Vulink 2001; Donlan *et al.* 2005). One of the most successful reintroductions of a wild species kept in captivity concerns the Przewalski's horse in Mongolia (Van Dierendonck & Wallis de Vries 1996). The “de-domestication” of large herbivores has been also included in research programs based on the restoration, preservation and management of natural ecosystems (Kampf 2000). In the Oostvaardersplassen reserve (6000 ha in the Netherlands), cattle and horses have been reintroduced and unmanaged for 20 years (Vulink 2001) in order to restore near-natural ecological processes in this ecosystem.

Among livestock, the domestication of horses is quite recent (about 6000 years ago). Several decades after their release, some horse populations are now considered as “wild” in North America and Europe (Berger 1986, Garrott & Taylor 1990). Several studies of feral populations of herbivores have focused on the impact of feralization in terms of reproduction (Hall & Hall 1988, Berteaux & Micol 1992). It has often been assumed that the process of feralization leads to a rapid return to wild-type social systems, and natural population dynamics. In Equids, this is supported by the fact that the structure and dynamics of feral horse social systems are similar to those of their wild relatives. However nothing is known about the mechanisms involved in the population dynamics – through variations in vital rates – of domestic animals released from human management. Another important point in the process of feralization is the general observation of biased sex ratios in reintroduced populations (Berteaux 1993). These sex ratios often reflect sex differences in mortality rates that could be due to the social structure, increased competition or higher sensitivity to environmental factors.

In this paper we describe the pattern of feralization in a herd of minimally managed domestic horses whose life histories and body condition were monitored on an individual basis for nine years (1975 – 1983). The study was set up in the Camargue (Southern France)

with 14 individuals in 300 ha of semi-natural habitat in order to allow them five years with abundant resources (1974 – 1979). At the end of this period the population was allowed to continue to increase, which provides an experimental test of the effects of density on horse population dynamics. The main response to “feralization” was therefore a strong increase in horse numbers, and its consequences are investigated through three major questions.

**First**, what are the main factors responsible for the observed changes in vital rates? As variations in body condition (or weight) can greatly influence survival and fecundities in large mammals (Gaillard *et al.* 2000b), we first explore which environmental variables most influenced the condition of horses. To understand the causes of changes in survival and fecundity (according to age class and sex), we then explore the relationships between environmental factors, biological variables and demographic parameters.

**Secondly**, what would be the future population trends of this population under no management? We therefore simulate annual population sizes after 1980 through a matrix model integrating density-dependent effects on demographic parameters. The main objectives of this modelling exercise are to follow the evolution of the adult sex ratio and predict the horse demography.

**Thirdly**, what is the pattern of the observed changes in vital rates, like survival and fecundity? It is expected that the horse population would respond to resource shortages through declines in vital rates according to the Eberhardt’s model (Eberhardt 1977, 2002). Juvenile survival should decline first, followed by fecundity in young females, then adult females. The last vital rate that should decline is expected to be adult survival, with females responding after males.

## **II - Material and Methods**

### 1 - Camargue horses

#### *1.1 - The population and the study area*

This study concerns a herd of Camargue horses living on 300 ha in the delta of the Rhône River (Southern France). The initial herd was composed of 14 horses in 1974; without any management this population increased until it reached its food ceiling in 1980. From 1981, horses in poor body condition were removed from the herd for ethical reasons: these

horses have been considered as dead in our annual survival estimates. In 1982 and 1983, managers also removed horses in order to rebalance the population sex ratio.

Data on annual rainfall are available for the nine years of our study (1975 – 1983). Research programs on feeding behaviour were also carried on this population and provided quantitative (herb biomass in tons) and qualitative (faecal crude protein “CPF” in Spring) information on food resources between 1975 and 1983 (Table 4.1).

Table 4.1. Data on horse numbers and condition, and rain and vegetation

Year	Condition (Spring)	Weight (Spring)	Density (ind/km <sup>2</sup> )	Herb (t)	Rainfall (mm)	Diet quality CPF (Spring)
1975	2	418	7.2	575	506	12.6
1976	2.2	413	8.5	515	628	11.4
1977	2.3	411	11	500	950	10.3
1978	2.4	408	15	485	816	9.6
1979	2.9	396	19	470	437	9
1980	3.3	375	24	365	777	10.2
1981	4.4	361	26	315	463	8.3
1982	4	325	20	265	405	8.3
1983	3.2	311	6.6	165	588	10

### *1.2 - Data on the horse population*

Body mass of adult female horses was measured in a Marechal balance in March and September each year from 1980 to 1983. For 1975-79, we used a linear regression to extrapolate the weight of females from their condition index (weight = -24.927\*condition + 467.838; R<sup>2</sup> = 0.9376, p = 0.0003). A visual condition score was noted for each individual (a very fat individual is scored as “1” and a very thin as “5”) by one observer in the middle of each month, using photographs for 1975-6, and field observations from September 1979. Here, we used the median of body condition observed on adult females in spring. In our analyses we therefore included the diet quality, and the body condition and weight of adult females measured or estimated in March between 1975 and 1983.

All horses were individually known, and births and deaths were recorded, so the parentage of horses was established each year from field observations and genetic analyses. Information on age- and sex-specific survival rates and fecundities was therefore available from 1975 to 1983 (Table 4.2). The population growth rate and the adult sex ratio were estimated from the size and composition of the herd each year.

Table 4.2. Data on demographic parameters for Camargue horses

Year	Male survival			Female survival			Female fecundity		
	Adult+SA*	Juvenile	Foal	Adult+SA*	Juvenile	Foal	Adult	SA*	Juvenile
1975	1	1	1	1	0.75	1	1	1	1
1976	0.8	1	1	1	1	1	1	1	0.66
1977	1	1	1	1	1	1	1	1	none
1978	1	1	1	1	1	0.9	0.8	1	0.7
1979	1	1	1	1	1	1	1	0.9	0.72
1980	1	1	0.71	0.94	0.87	0.9	1	0.9	0.55
1981	1	1	0.85	0.78	0.92	0.75	1	0.79	0.55
1982	1	0.85	0.71	0.8	0.62	1	1	0.75	0.1
1983	1	0.75	0.8	0.81	0.75	1	0.9	0.61	0

\* SA = sub-adult

To examine changes in vital rates we defined two study periods (1974-79 and 1980-83) based on an estimate of food limitation. The “annual production” (the change in weight of the herd, plus the weight of individuals born, exported or dead), increased until 1979, and then decreased (Fig. 6, p.18 in Duncan 1992b), leading us to conclude that the Camargue horses reached the food ceiling in 1979.

## 2 - Analysis and modelling

### *2.1 - Changes in survival rates and fecundities*

The changes in demographic parameters between the two periods defined above are tested through analyses of variance (or a Kruskal-Wallis test if there is no normality). The relationships between our different variables are measured through correlation coefficients (we used the Pearson coefficient when the distribution of the variable was normal, and the Spearman coefficient when it was not).

### *2.2 - Population modelling*

We simulate the future trends of the Camargue horse population – under no management – including density-dependent effects on demographic parameters. The managers removed horses during the last three years of this study. Horses in poor condition were relocated in another area and considered as dead in our analyses. In 1982 and 1983, managers started to remove animals in order to rebalance the sex ratio. In 1982 the population size after removals was 82. However out of the 21 horses removed to rebalance the sex ratio, 12 remained in the herd during the critical period (*i.e.* during winter) and were only removed

in April 1982. For this year we therefore corrected the population size by adding these 12 horses ( $N = 94$ ). In 1983, the sex ratio was balanced through considerable removals, and the population size cannot be used – even if corrected for removals – as the density was already artificially reduced during the previous year.

Our population model is a pre-breeding model (Leslie matrix), two-sex based and age-structured. We first examine the effect of density through the shapes of the relationships between vital rates and the population sizes from 1975 to 1982: we use the LOWESS program, a non-parametric smoothing program based on locally weighed regressions (Crawley 2002). We then fit polynomial regressions on all vital rates. The effect of density is therefore integrated in three parameters:

- 1- Sub-adult female fecundity:  $FECsa = -0.00004*N^2 + 0.0018*N + 0.9844$  ( $R^2 = 0.9498$ ;  $p = 0.0006$ ),
- 2- Adult/sub-adult female survival:  $SFadsa = -0.00008*N^2 + 0.0058*N + 0.9015$  ( $R^2 = 0.9474$ ;  $p = 0.0006$ ),
- 3- Foal male survival:  $SMfoal = -0.00004*N^2 + 0.0013*N + 1.0069$  ( $R^2 = 0.7428$ ;  $p = 0.0336$ )

In this model, we also apply a condition that constrains density-dependent parameters ( $FECsa$ ,  $SFadsa$  and  $SMfoal$ ) to be positive or null. We assume that the mean life expectancy is 25 years (Gross 2000), which means that in our model horses die when they are 25 years old. Three age-classes were used to estimate annual survival rates for both sexes: “foal” (0-1 year), “juvenile” (1-3 years-old) and “adult / sub-adult” ( $\geq 3$  years-old). For fecundity estimates, the “juvenile” age-class (2-4 years-old) did not include the yearlings and the last age class is divided into “sub-adult” (4-8 years-old) and “adult” ( $\geq 8$  years-old). Both survival and fecundity estimates correspond to mean values from 1980 to 1983 (during these 4 years the horse population was food-limited).

### **III - Results**

#### *1 - The causes of changes in vital rates*

##### *1.1 - Horse condition, density and food resources*

The adult female body condition in March is positively correlated to the annual herb biomass and its quality (CPf spring). The population density has a bad effect on female body condition (negative correlation) and is inversely related to the quality of food (Table 4.3). These results show that the condition of adult females depends principally on the quality and quantity of herb, and could be therefore also affected by intra-specific competition for resources.

The body weight of adult females is highly correlated to the annual herb biomass (Table 4.3); however there is no significant correlation between female weight and herb quality.

The quality of resources (CPf spring) is negatively correlated to the horse density (Table 4.3). This result could reflect an impact of horses on the herb quality, or could be a confounding effect due to the correlations between condition, CPf spring and density.

Table 4.3. Significant correlations between horse condition, density and environmental factors.

Variable 1	Variable 2	Pearson coefficient	p-value
condition	density	0.7514	0.0196 *
	herb	-0.7766	0.0138 *
	CPf spring	-0.8121	0.0078 **
weight	herb	0.9813	< 0.0001 ***
	CPf spring	-0.7255	0.0270 *

Significance codes: ‘\*’ < 0.05; ‘\*\*’ < 0.01; ‘\*\*\*’ < 0.001

### *1.2 - Demographic parameters and other factors*

Adult male survival is constant along the study period, except in 1976: there is therefore no significant correlation between this demographic parameter and environmental variables or density. The survival of young males (juveniles and foals) is positively correlated to adult female body weight and the quantity of resources. The survival of foal males also depends on female condition (Table 4.4) and is positively correlated to “adult / sub-adult” female survival ( $r_{\text{Pearson}} = 0.7520$ ;  $p = 0.0194$ ).

The survival rate of adult and sub-adult females depends on their own condition (and weight) and is positively correlated to the abundance of food resources. Juvenile female survival is related to adult female body weight, and foal female survival is negatively influenced by horse density (Table 4.4)

Adult female fecundity is not significantly influenced by environmental factors, condition status or density. Sub-adult fecundity is related to female condition (and weight),

but also to the abundance of food resources. Juvenile fecundity is affected by both adult female body weight and herb biomass (Table 4.4).

**Table 4.4. Significant correlations between demographic parameters and other factors**  
(<sup>§</sup> Spearman coefficient)

Demographic parameter	Factor	Pearson coefficient	p-value
SM juvenile	weight	0.7303 <sup>§</sup>	0.0311 *
	herb	0.7303 <sup>§</sup>	0.0311 *
SM foal	condition	-0.7593	0.0117 *
	weight	0.8184	0.0070 **
	herb	0.8142	0.0076 **
SF adult/sub-adult	condition	-0.8875	0.0014 **
	weight	0.9022	0.0009 ***
	herb	0.8142	0.0076 **
SF juvenile	weight	0.6767	0.0453 *
SF foal	density	-0.6943	0.0380 *
FEC sub-adult	condition	-0.7252	0.0271 *
	weight	0.9723	< 0.0001 ***
	herb	0.9628	< 0.0001 ***
FEC juvenile	weight	0.9509	0.0003 ***
	herb	0.9386	0.0006 ***

Significance codes: '\*' < 0.05; '\*\*' < 0.01; '\*\*\*' < 0.001  
Notation: M = male, F = female, S = survival and FEC = fecundity

### 1.3 - Changes between 1975-79 and 1980-83

The only parameters that are significantly lower after 1979 are the survival of foal males, adult females and sub-adult females, and the fecundities of sub-adult and juvenile females (Table 4.5). The juvenile survival rates of males and females also show similar trends, but differences are not significant ( $p = 0.09$ ).

**Table 4.5. Analyses of variance and Kruskal-Wallis tests on demographic parameters between period 1 (1975-79) and period 2 (1980-83).**

Parameter	Age class	Test	Mean (Period 1)	Mean (Period 2)	p-value
Male survival	Adult / Sub-adult	K-W	0.96	1	0.3711
	Juvenile	K-W	1	0.9	0.0935
	Foal	ANOVA	1	0.7675	0.0001 ***
Female survival	Adult / Sub-adult	ANOVA	1	0.8325	0.0012 **
	Juvenile	ANOVA	0.95	0.79	0.091
	Foal	ANOVA	0.98	0.9125	0.2721
Fecundity	Adult	K-W	0.96	0.975	1
	Sub-adult	ANOVA	0.98	0.7625	0.0068 **
	Juvenile	ANOVA	0.77	0.3	0.0294 *

Significance codes: '\*' < 0.05; '\*\*' < 0.01; '\*\*\*' < 0.001

2 - Model simulations

The adult sex ratio (% male;  $\geq 4$  years-old) was initially strongly female-biased at 17% in 1974, and increased to 63% in 1982. The model predicts a similar trend leading to a highly biased adult sex ratio, with 95% male after 10 years of simulation (Table 4.6).

Table 4.6. Changes in population size, growth rate and adult sex ratio during a ten-year simulation

Year	Population size	Population growth rate	Sex ratio (% male)
1980	67		0.41
1981	78	0.16	0.48
1982	89	0.15	0.54
1983	98	0.13	0.59
1984	105	0.10	0.65
1985	111	0.07	0.73
1986	116	0.05	0.80
1987	122	0.04	0.87
1988	127	0.05	0.91
1989	134	0.05	0.95

Between 1975 and 1979, the Camargue horse population showed a high mean annual growth rate ( $r$ ) of 28%, and from 1981 the population decreased ( $r < 0$ ) because of annual removals. After 10 years of simulation, our model integrating density-dependence of demographic parameters leads to a strong decrease in population growth (from 16 to 5%; Table 4.6). If we run the model for 100 years, this decrease in population growth rate would lead the Camargue horses to reach a maximum population size of 174 horses after 18 years, and then stabilize at a threshold of around 160 individuals (Figure 4.1). The model predictions indicate that after 20 years, the population growth rate would be quasi null, the foal/mare ratio would decrease from 0.78 to 0.30 foal/mare/year reflecting a strong decrease in the recruitment (from 21 to 0 foal/year), and the adult sex ratio would reach 100% males.

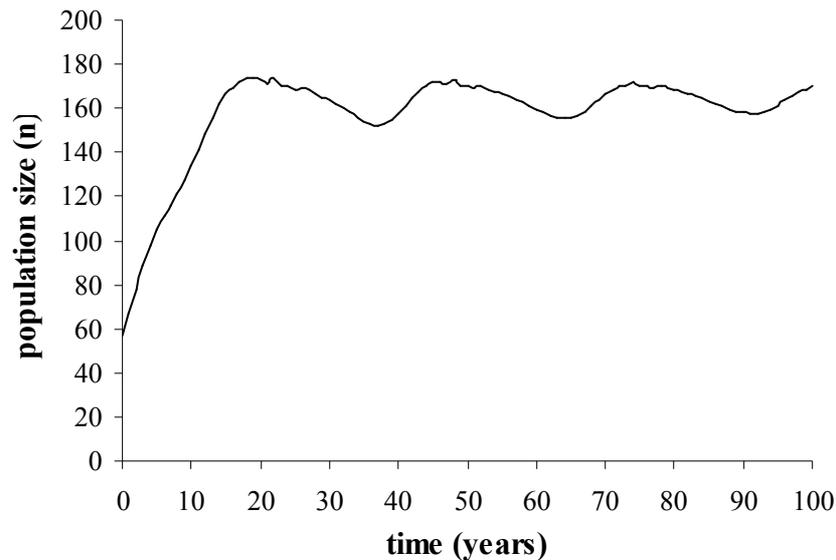


Figure 4.1. Simulated demography of Camargue horses after 100 years.

### 3 - The pattern of changes in vital rates

The vital rates are affected by density following this sequence: first the fecundity of young females, then the survival of foal males, the female survival rates (adult, sub-adult and juveniles), and finally the survival of juvenile males (Fig. 4.2). This sequence is not in agreement with the predictions of Eberhardt's model. In particular, the survival of young horses appears to react later than expected.

According to our previous results, during the 4 years of food-limitation (1980-1983), the survival of mature males (mean  $SM_{adsa} = 1$ ) is not affected by density as those of females (mean  $SF_{adsa} = 0.83$ ), which leads to an unequal mortality between sexes. In juveniles, female survival is first affected by density (mean  $SF_{juv} = 0.79$ ) and more strongly than males (mean  $SM_{juv} = 0.9$ ). Among foals, males are more susceptible to the increased density compared to females (mean  $SM_{foal} = 0.77$ , mean  $SF_{foal} = 0.91$ ).

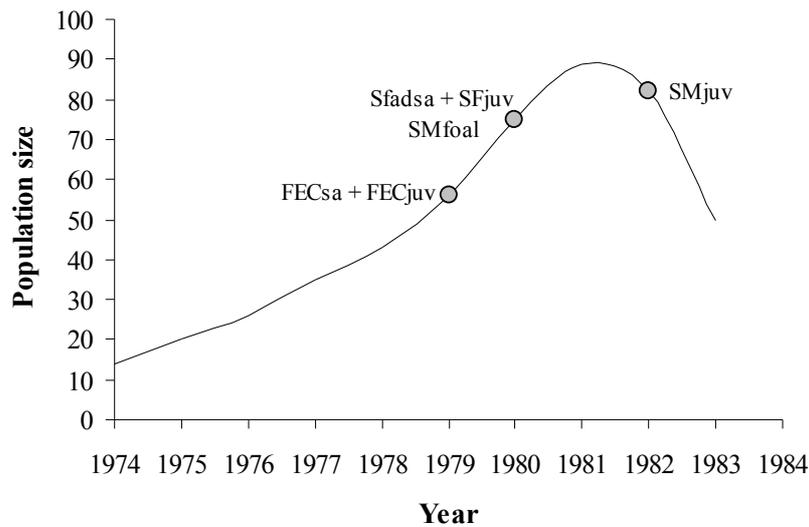


Figure 4.2. Demography of Camargue horse. The grey dots indicate the starting point of density-dependent effect on vital rates: survival of juvenile males (SMjuv), survival of adult / sub-adult females (SFadsa) and juvenile females (SFjuv), survival of foal males, and fecundity of sub-adults (FECsa) and juveniles (FECjuv)

Although domestic horse is not a dimorphic species, we observe differences between sexes. Adult females are clearly more affected than males, and this observation is also reflected through variations in adult sex ratio (% males) that was initially biased towards females (17% in 1974) and then changed in favour of males (63% in 1982).

#### IV - Discussion

These Camargue horses were released at a low density in an area without predators and including a large amount of resources. Their immediate response was therefore a strong increase of the population during the years following their return to the wild ( $r = 28\%$  for 1975-79): after 5 years under no management, horses reached their food ceiling and the first declines in vital rates in response to increased density appeared.

The causes of changes in vital rates have been investigated through interactions between different factors. The survival of adult females is linked to their body condition, which in turn depends strongly on food resources (in terms of quantity and quality). This strong dependence on food resources is also reflected by high seasonal variations in adult female body condition. In 1982-83 – two years with major food shortages – adult females experienced high weight losses between spring and winter (Duncan 1992b). These field observations are in agreement with the significant decrease of mature female survival before

and during the food limitation (1975-79 and 1980-83; Table 4.5). Moreover, mares increased the length of lactation – and its associated costs – between 1975 and 1983. The survival of male foals clearly depends on lactation, *via* the body condition of their mares. They also present a significant decline in their survival before and during the food limitation period (Table 4.5). Surprisingly the survival of female foals is not related to the mare body condition, but they seem to be more affected by population density. However because of the lack of data on parental care, the relatively high survival of females (0.91 for 1980-1983) compare to males (0.77 for 1980-1983) during their first year of life cannot be attributed to a higher investment of mares in female offspring. Since in the Camargue colts nursed longer than fillies (Duncan *et al.* 1984), it could explain the apparent stronger dependence between the nutritional status of mares and the survival of their male offspring. Patterns of parental investment have been investigated in horses, and show that females in good body condition tend to invest more in sons (Cameron & Linklater 2000). In the Great Basin population, Berger (1986) also noticed that male offspring were nursed longer than females.

In Camargue horses, the reproduction of young females was clearly affected by the increase in density. Adult females did not show a decline in their fecundity even during the period of food limitation. However during this period the fecundities of sub-adult and juvenile females significantly changed with respective declines of 22 and 61%. Young female fecundities are both related to adult female condition, which is linked to the effect of food shortage. Thus, the main factor directly affecting fecundity rates is probably the abundance of food resources. Moreover, in the Camargue, access to resources is partly based on a hierarchy within herds (Duncan 1992b): older mares generally dominate the younger ones and are the first ones to have access to food resources.

All these changes in demographic rates are also linked to the specific social structure observed in this population, including variations in social system. The initial composition of the herd influenced the social behaviour of Camargue horses. Initially, the herd was female-biased (17% male), which could have favoured and accelerated the return to the social structure of wild equids, with adult females and their offspring gathered in families leading by one (or two) stallions, and bachelors in different groups (Klingel 1982; Boyd & Keiper 2005). If the initial sex ratio had been balanced, the competition between males for access to reproductive females would have been greater. Indeed, immediately after their release, Camargue horses formed two groups: one bachelor group and one harem headed by the dominant stallion. Year after year the number of harems increased (7 family units in 1979),

and this population quickly exhibited a wild-type social system. Because of the increasing proportion of adult males in this herd we expected an increase in the number of harems with a decrease in harem size. Moreover, the family structure was very stable because no horse changed family between 1978 and 1983 (Duncan 1992b). Such stability in the social structure could have consequences on reproductive rates in horses. It has been shown that females belonging to unstable bands have significantly lower reproductive success than those from stable bands (Berger *et al.* 1983). This result could explain the relatively high foaling rate observed in Camargue females. Moreover, the selection along generations of domestic horses for adult females with the highest reproductive potential probably affects the trade-off between reproduction and survival, leading adult mares to invest more in their reproduction. On the other hand, as the family structure was very stable, the costs associated with the defence of a harem were abnormally low, and the very high adult survival in males resulted also from the fact that all males in this herd knew each other and the inter-male competition was nearly absent: threats between adult stallions were very rare (0.04 threats / horse / year; in Duncan 1992b). This low competition between adult males can also result from the process of domestication that generally tends to select the least aggressive animals. These conditions led to sex differences in adult survival, and the sex ratio became clearly male-biased (63% males in 1982) before managers decided to remove animals and rebalance the proportions of males and females in this herd.

The modelling allowed us to predict the demography of this horse population for 10 more years without any human management. Three vital rates seemed to be particularly affected by density: the survival of foal males and adult females, and the fecundity of sub-adult females. However, our study period was quite short: as the managers started to rebalance the population sex ratio by removals in 1982 and 1983, we were able to correct the population size in 1982 and had to remove 1983 from our analyses. For this reason, the simulation of density effects on horse vital rates is approximate, and we preferentially considered the simulated trends rather than the model estimates. As suggested by field data, the adult sex ratio should become strongly male-biased (95% males after 10 years). However it is improbable that it would reach 100% males after 20 years, as the increased proportion of males in this population should lead to an increasing competition for access to females and the defence of harems by stallions. Other “wild” horse populations present generally a female-biased sex ratio when food resources are not limited (Table 4.7): it was the case for Camargue horses at the beginning of the study (Duncan 1992b), but also for the Great Basin (Berger

1986) and Pryor Mountain horses (Garrott & Taylor 1990). When the populations are food-limited – as for Camargue horses after 1980 and Sable Island horses (Welsh 1975) – the adult sex ratio is clearly male-biased. These observations indicate that when food resources are limited the costs of reproduction for females are higher than the costs of competition for males. However this result cannot be generalized to harvested populations of wild equids or in ecosystems including large predators (Berger 1983).

Table 4.7. Comparison between demographic parameters (mean values) derived from different “wild” horse populations monitored on an individual basis (including this study)

	Great Basin (a)	Pryor Mountain (b)	Camargue (c)	Camargue model (d)	Kaimanawa (e)
Years	1979 - 1983	1977 - 1986	1975 - 1983	1980 - 1989	1994 - 1998
Time (years)	5	10	5	10	4
Population size	58 - 149	86 - 181	14 - 89	67 - 134	413
Growth rate (r)	0.188	0.113	0.277 <sup>(1)</sup>	0.085	0.092
Adult sex ratio (% males)	43	34	36 <sup>(2)</sup>	69	48
Male adult survival	0.95	0.96	0.98 <sup>(3)</sup>	1	0.97
Female adult survival	0.95	0.99	0.93 <sup>(3)</sup>	0.60	0.94
Male foal survival	0.92	0.92	0.9 <sup>(3)</sup>	0.69	0.79
Female foal survival	0.92	0.95	0.95 <sup>(3)</sup>	0.91	0.87
Foaling rate (adult female)	0.9	0.55	0.97 <sup>(3)</sup>	0.58	0.61

Data sources: Berger 1986<sup>(a)</sup>; Garrott & Taylor 1990<sup>(b)</sup>; Duncan 1992b<sup>(c)</sup>; this study<sup>(d)</sup>; Cameron *et al.* 2001<sup>(e)</sup>  
 Mean values for 1975-79<sup>(1)</sup>; for 1974-82<sup>(2)</sup>; for 1975-83<sup>(3)</sup>

This study on Camargue horses is particularly interesting as it is based on an individual monitoring of the whole population, which means that precise demographic rates are known. Among studies on “wild” horses, three were individually-based (Table 4.7). The high vital rates observed in Camargue horses before 1980 led to a high population growth rate (28%). This rate probably represents the maximum potential growth rate of a horse population under favourable conditions (no predators, no disease, and a sufficient food supply all year). There was also a high growth rate in the Great Basin (19%), but lower than in the Camargue: Berger (1986) showed that social competition reduced the recruitment rate in this Northern American population. Different factors can lead to a lower population growth rate in “wild” horses: the negative effects of density on demographic parameters in Camargue horses reduced their population increase to 8.5% per year (simulation on 10 years). In Kaimanawa horses (Cameron *et al.* 2001) a low recruitment due to high foetus losses (31%) allowed only 9% increase per year. On average after 10 years of simulation, the foaling rate of Camargue horses should be similar to those of the Kaimanawa population (0.6). The recruitment rate (*via* foetus losses, low juvenile survival, or low fecundities) should therefore have a

considerable impact on the population dynamics of “wild horses”. Another important point was that in the Camargue and the Great Basin, where population growth rates were high, there was no important competitor for horses – like grazing bovids. In African ecosystems, where medium-sized ruminants and large predators are still present, zebra populations generally present low growth rates and are very stable.

The vital rates of Camargue horses are quite similar to those of other “wild” horses. In North American studies, horses do not live with large predators and show high survival rates like in the Camargue ( $> 0.9$ ). The foaling rate is more variable between these different populations, and is particularly high in Camargue horses. When survival is high, the foaling rate seems to be a critical parameter in horse population dynamics, and herds with a high recruitment (resulting from high foaling rates) also have high population growth rates (the Great Basin and the Camargue – before 1980) contrary to herds with lower foaling rates (Pryor Mountain and Kaimanawa). A linear regression performed on the four populations compared here and our model simulation tends to confirm this relationship:  $\text{growth rate} = 0.3882 * \text{foaling rate} - 0.1293$  ( $n = 5$ ,  $R^2 = 0.8831$ ,  $p = 0.0176$ ; Shapiro test:  $p = 0.2458$ ). Our model on Camargue horses leads to a low population growth rate partly because of a strong decrease in the annual foaling rate (21 foals / year in 1980 and only 1 after 12 years of simulation). This observation results from density-dependence, which clearly induced decreases in vital rates, particularly in the survival of adult females and in sub-adult female fecundities.

Interestingly the model simulations predict that Camargue horses would reach a threshold of about 160 individuals after 20 years of simulation. This population size is probably over-estimated as the increase of male competition suggested by the biased sex ratio, the strong depletion expected of food resources, and the potential effects of density on all vital rates (except for SFadsa, SMfoal, and FECsa) cannot be modelled here. We can therefore predict that, after reaching their maximum population size (around 160 individuals, *i.e.* more than 40 horses / km<sup>2</sup>), the population would experience a major die-off: at carrying capacity the Camargue population should therefore present a very low density, similar to other “wild” horses (4 horses / km<sup>2</sup> in the Great Basin, and 8 horses / km<sup>2</sup> in Kaimanawa).

We finally compared the sequence of demographic parameters affected by density to Eberhardt’s predictions (Eberhardt 1977). If we consider one sex and one parameter (survival or fecundity), young horses tend to respond first. However foal and juvenile survival rates are not affected first as predicted by Eberhardt. Fecundities of young females are the most

sensitive. The main difference concerns the adult age class where males are not affected, but as there is no data on male body condition and weight, we cannot really test the effect of density on their condition status. However, adult females are clearly affected by the increase in density. And the comparison of growth between sexes leads to a quicker slowing down in growth for females than for males, indicating that food limitation affects females more than males (Duncan 1992b). The higher adult mortality in females rapidly leads to a male-biased sex ratio: as suggested by our previous results, the costs of lactation should not be counterbalanced by costs due to inter-male competition or harem defence that are abnormally low in this population.

Consequently field observations clearly showed that after their release in the wild, the Camargue horses returned rapidly to a wild-type social system, but the very low costs of inter-male competition in harem defence and the decrease of food resources led to an adult sex ratio strongly biased towards males. Our study is the first one to investigate the consequences of feralization on demographic parameters. Our analyses highlight the importance of food resources – particularly for females – and foaling rates on the horse population dynamics. In North America, horses are usually considered as pests because they can increase rapidly and strongly when the food supply is sufficient and when there is no predator in the system. In North America, the management of “wild” horses has been largely based on removals. This method has been proved to be efficient when the choice of animals was made according to scientific data on the horse population dynamics. Without such information, removals could also lead to strongly biased sex ratios and have therefore consequences on horse behaviour and survival. The outcome of removals in terms of population dynamics is less predictable compared to direct manipulations of reproductive rates in “wild” horses (Gross 2000). The development of contraceptive methods has therefore been used in the management of large herbivore populations. In Wyoming and Colorado fertility controls initially based on modelling have been successfully applied to horse populations (Bartholow 2004). Cameron *et al.* (2001) also concluded that the use of contraceptive methods to control the Kaimanawa horses would be very efficient. Finally, this study also demonstrates the major role of adult sex ratio in mammal population dynamics. It could be possible to manage large herbivore populations by manipulating sex ratios. Variations in sex ratio can effectively reflect changes in population size, but many factors can bias the “change-in-sex ratio” estimation (Solberg *et al.* 2005). The feralization in Camargue horses clearly favoured males compared to females in

this study. However, if the Camargue horses had stayed unmanaged, their adult sex ratio highly biased towards males would probably have been balanced after several years, increased competition between males leading to similar survival rates between sexes, as in other “wild” horse populations.

### **Acknowledgements**

We would like to thank people from “La Tour du Valat” who collected data on Camargue horses during all these years. We are also very grateful to Pierrick Blanchard, Christophe Bonenfant and Géraldine Fleurance for their critical and constructive comments on a previous version of the manuscript.

## Discussion



*May you build a ladder to the stars  
And climb on every rung  
May you stay... forever young*

*...  
May you always be courageous  
Stand upright and be strong  
And may you stay... forever young*

Bob Dylan

## Synthesis

The understanding of factors limiting and/or regulating animal populations is always a challenge and a difficult task for ecologists, particularly when it concerns ungulate populations living in natural complex ecosystems (*i.e.* multi-predator multi-prey systems) and variable environments. However, identifying the causes of variations in large herbivore abundance is a central issue not only in terms of species conservation, but also for the management and restoration of natural ecosystems. In this thesis, my work has been focused on the population dynamics of wild equids, especially plains zebra (*Equus quagga*). In spite of their central role in African ecosystems there is relatively little information about the regulation / limitation of zebra populations (Hack *et al.* 2002). Using different approaches at different scales (individual, population, community), I have tried to assess the factors which are most likely to cause variations in plains zebra populations.

The first chapter highlighted the demographic processes leading to the population trends of three ungulates through long-term studies in the Serengeti ecosystem, Tanzania. To understand why the zebra population remained so stable, we used a comparative approach to the population dynamics of zebra and two grazing bovids (wildebeest and buffalo). Through model simulations, this study clearly identified the demographic process that limits the Serengeti zebra population: the zebra first-year survival rate is very low compared to that of wildebeest and buffalo. However, the causes of high juvenile mortality in this zebra population are not known. From variations in the abundance and the diet of large predators (lions and hyenas), we estimated the offtake in the three prey populations considered here, and showed that the predation pressure was probably most important on zebra across the study period. However, more accurate data on the proportion of prey in different age classes are needed to assess the real impact of large predators on the population dynamics of these ungulates. So the ecological process that leads to low survival in foals is not clearly identified, but according to the spatial distribution of zebras (Maddock 1979) and their timing of birth (Klingel 1969b, Smuts 1976a), we suggest that predation can play an important role in the limitation of the Serengeti zebra population, notably through its impact on young individuals. More interestingly this study highlighted two major points. First, predation should be given more consideration in African ecosystems, as there could be an important role of large predators in the regulation and/or limitation of some ungulate species. Previous studies of

African ungulates have focused on the importance of food resources for medium-sized herbivores that live in such variable environments (Sinclair 1977, Mduma *et al.* 1999). The dry season with its low food supply is generally crucial for the survival of African herbivores, and the impact of predation on these populations has been considered relatively less important. There is little evidence for the regulating or limiting role of large predators in African ecosystems; however some ungulate populations – like the roan antelope in Kruger National Park (Harrington *et al.* 1999) – are strongly influenced by predation. The second important point raised by this study is the real lack of accurate data on the demographic parameters – particularly sex- and age-specific survival and fecundity rates – of African mammal species. Most available survival rates are derived from life tables. However this method is biased, particularly concerning the estimates of juvenile survival, as it relies on the age of collected skulls, and the carcasses of small animals are rarely found. Moreover in such stochastic environments as African savannas, vital rates show a high variability (particularly in juveniles), which can have important consequences in terms of population dynamics (Gaillard *et al.* 2000a). For African ungulates, there is currently no study of population dynamics based on a capture-mark-recapture method with accurate estimates of survival rates.

The analysis of the Serengeti ungulates therefore led to a study on the relative importance of food resources and predation on the abundance of plains zebra, wildebeest and buffalo across 23 African protected areas (see Chapter 2). In order to provide accurate data on zebra survival rates, a capture-mark-recapture study on plains zebras in Hwange National Park (Zimbabwe) was set up in July 2004 (see preliminary results in Chapter 3).

In chapter 2 the effects of rainfall and lion density on the relative abundance of zebra and grazing bovids were investigated across African ecosystems. The aim of this study was to highlight the general patterns that most influence the population sizes of plains zebra, wildebeest and buffalo coexisting in different ecosystems. The objective was to test if zebras are generally less sensitive to food shortage and more sensitive to predation than grazing bovids, as is apparently the case in the Serengeti ecosystem (Grange *et al.* 2004) and in Kruger National Park (Redfern *et al.* 2003, Owen-Smith *et al.* 2005). The significant positive correlation between lion and hyena densities allowed us to use lion densities across ecosystems as an index of large predator densities. The analysis of bottom-up effects (*via* annual rainfall and soil richness) confirmed the results of previous studies on African large

herbivores (Fritz & Duncan 1994), but by focusing on three ungulate species this study provides more information on the relative impacts of food quality and quantity on the abundance of zebra, buffalo and wildebeest. Such information is important to understand if bottom-up processes are sufficient to explain the differences in abundance between these ungulate populations, and then to assess the mechanisms that allow their coexistence. This comparative study showed that buffaloes – which are heavier and classified as roughage feeders – are affected by the amount of resources, and they are also influenced by food quality. Wildebeests are clearly dependent on the quality of resources; zebras are too, but to a lesser extent. In accordance with our predictions, wildebeests appear more closely dependent on food resources than zebras; buffaloes are intermediate. Equids and grazing bovids are potential competitors, and their strategies on food resources are now better understood in Europe through studies on horses and cattle (Duncan *et al.* 1990, Ménard *et al.* 2002). Despite this, there is still little information on the impact of competition for food resources on the relative abundance of zebras and African grazing bovids of similar body size. Studies on the comparative feeding behaviour of zebra, wildebeest and buffalo are therefore required to measure the relative importance of food resources for these three species, and to understand how they can coexist on the same resource (grass). It is necessary to compare their feeding preferences at different scales (habitat, vegetation type, plant species and plant part), but also to assess precisely the body condition of these animals, particularly during dry periods. A preliminary analysis based on the spatial distributions of zebra, wildebeest and buffalo at different scales in Botswana (country, region, habitat, vegetation types) has already shown that the overlap between these species, and particularly between zebra and wildebeest, decreases at smaller scales (unpublished data).

The analysis of predation presented the shape of the lion numerical response to large herbivores across African ecosystems. This response is linear at the level of mesoherbivore communities, and probably also when only one prey species is considered. When we consider the comparative proportion of zebras to grazing bovids (ratio  $Z/BW$ ), it appears that zebras tend to be relatively more abundant in ecosystems with low predator densities. The linear model between the  $Z/BW$  ratio and lion density does not explain a large part of the variance, but we showed that the decline of this ratio with the increase of lion density cannot be explained by rainfall or competition with grazing bovids. It is therefore probable that zebra populations tend to be more influenced by “top-down” processes compared to wildebeest and buffalo populations. This assumption is only valid at a large scale, as regulating/limiting

factors acting on medium-sized ungulates can vary greatly between ecosystems. However, a general view of the composition and structure of African ecosystems is always interesting and useful to understand general patterns shaping mammal communities.

In chapter 3 preliminary results of the first study on the population dynamics of plains zebras based on capture-mark-recapture (CMR) are presented. The observations on the social system in this zebra population are compared to previous studies and the first survival estimates are presented and discussed. The mean family size is similar to previous results from other parks. The most interesting result concerns the stability of family groups: contrary to previous studies (Klingel 1967, 1969a, Smuts 1976b), the adult composition of family groups is very unstable in Hwange. Several factors could explain this relative instability. In this population the incorporation of adult females into new family groups often results from the disappearance of their own family stallion. In 3 cases out of 5, not the whole group, but some of the adult females and their offspring were found in new families. This seems to indicate that the family stallion has died because adult males rarely abandoned their females except when they are predated or when a new stallion took over the whole family. More data are needed to confirm this observation, but predation or disease could play a role in the stability of family groups in this zebra population. The densities of lion and spotted hyena in the whole park are not very high; however many lion prides and hyena clans are concentrated around water holes where the herbivore densities are also high during the dry season. The predation pressure could therefore be relatively high in such areas. It is also difficult to estimate the impact of diseases on zebra mortality as there are very few data on this in Hwange. The causes of the instability of zebra family groups remain to be identified, which should be possible after more fieldwork.

The first estimates of survival were obtained for adult males (family stallions), adult females, yearlings, and foals. The sample sizes are unfortunately too small to give accurate estimates. However the first estimate of adult male survival is in agreement with previous estimates derived from life tables on other zebra populations (Skoog & Gogan 1970, Spinage 1972, Smuts 1976b, Monfort & Monfort 1978). Because of the social structure of plains zebras it is possible that adult males from family groups or bachelor herds do not present the same survival rates. It would therefore be very interesting to include bachelor males in this database. The estimate of adult female survival is also similar to previous data on other zebra

populations. One major finding of this modelling exercise is that the social structure must be considered when we have to estimate vital rates through a CMR method. According to the particular social structure of plains zebras, the adult mares' recaptures are not independent within a family group and not considering family groups leads to severely biased estimates of survival. The first estimate of foal survival is based on a small sample size, but is in agreement with my field observations and also highlights an effect of family groups on the probability of capture. The major problem of this study is that I am currently not able to estimate the neonatal mortality of zebra foals. Klingel (1969a, b) had the same problem, and also obtained a high foal survival. To correct this bias it is therefore essential to assess the reproductive status of zebra mares. Adult female pregnancy will be determined through faecal samples during future fieldwork sessions.

Even if the results presented in the chapter 3 are only preliminary, this study of zebra population dynamics is promising as I obtained a considerable amount of data after only one and a half years of monitoring, and as the "recapture" based on photo-identification works very well. The other important point is that I obtained a realistic population model including the first vital rates obtained during my study period. The CMR method can therefore be widely applied to estimate age- and sex-specific survival rates in plains zebra populations.

In Europe most wild species of large mammals are now extinct, and the introduction of domestic herbivores to replace their wild relatives is now viewed as a solution to restore wildlife communities (Gordon *et al.* 1990, Kampf 2000, Vulink 2001). A major problem is therefore to manage these populations: feral animals generally return rapidly to their "wild-type" social systems, but little is known about the population dynamics of domestic herbivores during the process of "feralization". In chapter 4, we investigated the consequences of feralization for the demographic rates of Camargue horses. The immediate result after the release of 14 horses to the wild was a strong increase in their numbers, rapidly leading to density-dependent effects on the population vital rates. However, contrary to Eberhardt's predictions, the juvenile survival was not affected first. And interestingly adult females were more affected than males, who did not show any decrease in survival. These differences in mortality between sexes rapidly led to a strongly biased sex ratio.

This study shows that during feralization the population dynamics of Camargue horses tended to return to a natural wild-type, but not entirely. Artificial selection can explain such differences. First, the very high survival rates of adult males are probably due to weak male-male competition because of the rarity of threats between adult stallions (Duncan 1992b). This lack of aggressiveness results from the process of domestication and the fact that all horses knew each other at the beginning of the experiment. In domestic horses, females have been selected for reproduction, which can explain why adult fecundity was not affected, even during the period of highest horse densities. However, adult female survival significantly declined during the study period. In the wild, females have to make trade-offs between survival and reproduction, and when resources are scarce the reproductive success is generally well reduced (*e.g.* conception rates of plains zebra: Klingel 1969b, Smuts 1976a). The main consequence of artificial selection was a higher sensitivity of female horses to food shortage compared to males, leading to biased sex ratios. In this particular example, it is clear that an effective control of adult sex ratios is necessary to maintain this population on a long-term basis, unless differences in adult survival are counterbalanced by an increase in male mortality due to higher competition for females. Camargue horses cannot therefore be used to restore large mammal communities without any human management. It is also probable that several generations are necessary to allow these Camargue horses to exhibit the same “quasi-natural” population dynamics as feral horses (*i.e.* with competition between adult males for reproduction, and females that do not reproduce when environmental conditions become harsh).

## Conclusions and perspectives

This thesis has contributed to improve knowledge on the regulating/limiting factors acting on plains zebra populations. The use of a comparative approach to study the population dynamics of zebra and grazing bovids has provided a new perspective, and the development and generalization of such comparative studies appears essential to identify the demographic factors regulating or limiting mammal populations. This could also help to understand the underlying mechanisms that allow coexistence between equids and bovids within ungulate communities. The comparison of the “bottom-up” and “top-down” effects influencing several coexisting populations of zebra and grazing bovids have also helped to assess general patterns in the abundance of these African ungulates. One major result is highlighted by the first two chapters of this thesis: predation appears to play an important role in the population dynamics of zebras. However the current data available on large predators do not provide a clear assessment of their real impact on the demography of plains zebras. There is therefore a real need for coupled population models between zebras and their predators (principally lion and spotted hyena). Linking the population models of other grazers, such as wildebeest, could also be very useful. Given the complexity and species richness of African mammal communities, it might seem very difficult to realize such a study on the predator-prey dynamics. However, the zebra study in Hwange National Park (see Chapter 3) has already proved that with minimal costs it is possible to monitor efficiently a zebra population, and studies on large predators coupling diet analyses (through faecal samples) and monitoring *via* collared individuals can provide accurate data on their impact on prey populations. To test the assumption that zebras are more sensitive to predation than grazing bovids of similar body size it would be useful to compare the demography of these ungulates in parks that experienced a removal of large predators. Such an experiment is hardly conceivable for ethical reasons, but large predators were partially removed from several ranching areas in East Africa (*e.g.* around Narok District; Norton-Griffiths pers. comm.), which could provide suitable data to test my hypothesis.

However, even if predation appears to be an important factor that can limit zebra populations (see chapters 1 and 2), two other ecological factors could also play a role and have to be considered. This thesis has also pointed out the lack of knowledge concerning the relative importance of disease and social behaviour for the population dynamics of plains zebra. There is still little information on the effect of diseases on zebra survival, and the collection of blood samples is now required to check for parasitic loads and viruses in zebra

populations. A systematic autopsy of zebra carcasses found in the field would also help to estimate the impact of disease and parasitism on zebra mortality rates. Studies of captive plains zebras also showed that infanticide can occur in this species (Pluhacek & Bartos 2000, Pluhacek *et al.* 2006). Several reports of foal infanticide in wild horses (Ryder & Massena 1988) and Camargue horses (Duncan 1982) indicate that this behaviour also occurs in other equid species. Even if there is little information on this behaviour in wild populations of zebras, one case has been reported in mountain zebra (Penzhorn 1984) and one in Hartmann's zebra (Joubert 1972), suggesting that it could also occur in plains zebra. According to the particular social system of plains zebras and wild horses (harem structure), it is actually possible that infanticide has been selected as a means to increase the fitness of family stallions *via* their reproductive success.

The third interesting point in this thesis is that the lack of accurate data on vital rates in zebra populations can easily be remedied through capture-mark-recapture studies based on the individual stripe patterns of plains zebras. As explained in Chapter 3, the first results presented here are only preliminary and more data are clearly needed, but this study proved that such a method works for the study of population dynamics of plains zebra without requiring sophisticated logistics. The main problem is to estimate the first-year survival rate: it is therefore necessary to determine the importance of neonatal mortality through the assessment of adult female pregnancy status. The future computerization of the individual recognition system should allow us to increase considerably the current sample size and to improve the fieldwork efficiency. The next step will be to develop this approach for other zebra populations in order to compare their population dynamics under different environmental conditions.

Once the regulating/limiting factors acting on animal populations have been determined, the management of wildlife communities can be greatly facilitated and will be particularly efficient to control population density under various environmental conditions. For example, if an ungulate population is mainly affected by predation, it will be necessary to carefully control the predator densities to avoid the extinction of the prey. The presence or introduction of alternative prey can also reduce the impact of generalist predators on one particular prey. This knowledge on population regulation or limitation is therefore essential for the conservation of mammal species, which is an important economic issue in African countries. In Europe and Northern America, the current problem of wildlife managers and

ecologists is quite different: it concerns the preservation, but above all, the restoration of natural ecosystems. The introduction of large domestic herbivores is now used in Europe to restore ungulate communities (Kampf 2000). It is therefore important to know the consequences of feralization for the population dynamics of these herbivores. The study on Camargue horses has highlighted the importance of artificial selection and its consequences for the population dynamics of domestic animals. The high differences in mortality rates between the sexes led rapidly to strongly biased sex ratios, and the resulting population dynamics was different from wild populations in natural ecosystems. Camargue horses could therefore be used as surrogates for wild horses only under human management because such a low proportion of females can lead to population extinction on a long-term basis. Further, even after several generations in the wild it is not sure that these animals will exhibit “natural” population dynamics. Domestic horses, however, can be considered as engineers for grassland management: they can be used effectively in combination with cattle to maintain a high biodiversity in grasslands through their differential use of vegetation (Ménard *et al.* 2002).

The last chapter of this thesis clearly showed that the restoration of natural ecosystems with large herbivores is not a simple issue. Human management is often necessary, and the major problem is to find suitable species and suitable areas for reintroductions. As large herbivores, equids require large areas of land in order to sustain their populations. One major current threat to wild equids is the loss and fragmentation of habitat. Even if the plains zebra is not considered to be an endangered species, some populations have been extirpated from their range during the last decade. This underlines the urgent need for research on the population dynamics of African mammals still living in their natural habitats. A good understanding of the regulation and limitation within such animal populations will help to predict their population trends under known environmental conditions and is the first stage before planning for future reintroductions or translocations in natural ecosystems.

## **References**



## References

---

- Asa, C.S., Bauman, J.E., Houston, E.W., Fisher, M.T., Read, B., Brownfield, C.M. & Roser, J.F. 2001. Patterns of excretion of fecal oestradiol and progesterone and of urinary chorionic gonadotropin in Grevy's zebras (*Equus grevyi*): Ovulatory cycles and pregnancy. *Zoo Biology*, 20:185-195.
- Atwell, C.A.M. 1982. Growth and condition of blue wildebeest in Zululand. – *South African Journal of Wildlife Research* 12: 63-70.
- Bartholow, J. M. 2004, An economic analysis of alternative fertility control and associated management techniques for three BLM wild horse herds, U.S. Geological Survey, Biological Resources Discipline, Open File Report 2004-119.
- Bastian, C.T., Van Tassell, L.W., Cotton, A.C., Smith, M.A. 1999. Opportunity costs related to feral horses: A Wyoming case study. *Journal of Range Management* 52:104-112
- Bauer, H. 2003. Lion conservation in West and Central Africa: integrating social and natural science for wildlife conflict resolution around Waza National Park, Cameroon. PhD thesis, Leiden University, Leiden
- Bauer, H. and van der Merwe, S. 2002. The African lion database. Report for the African Lion Working Group. Available on-line at [<http://www.african-lion.org>].
- Begon, M., Harper, J.L., Townsend, C.R. 1986. Ecology. Individuals, populations, and communities. Sinauer Associates Inc., Publishers,
- Bell, R.H.V. 1970. The use of the herd layer by grazing ungulates in the Serengeti. Animal populations in relation to their food resources. Blackwell, Oxford
- Bell, R.H.V. 1971. A grazing ecosystem in the Serengeti. *Scientific American* 224:86-93
- Bell, R. H. V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. - In: Huntley, B. J. and Walker, B. H. (eds.), *Ecology of Tropical Savannas*. Springer, pp. 193-213.
- Ben-Sahar, R., Coe, M.J. 1992. The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. *Oecologia* 90:422-428
- Berger, J. 1983. Predation, sex-ratios, and male competition in equids (Mammalia : Perissodactyla). *Journal of Zoology* 201, 205-216.
- Berger, J. 1986. Wild horses of the Great Basin. Social competition and population size. The University of Chicago Press, Chicago & London
- Berger, J., Kock, M., Cunningham, C. & Dobson, N. 1983. Chemical restraint of wild horses: effects on reproduction and social structure. *Journal of Wildlife Diseases* 19, 265-268.
- Berteaux, D. 1993. Female-biased mortality in a sexually dimorphic ungulate: feral cattle of Amsterdam Island. *Journal of Mammalogy*, 74:732-737.
- Berteaux, D. & Micol, T. 1992. Population studies and reproduction of the feral cattle of Amsterdam Island. *Journal of Zoology* 228, 265-276.
- Bonyongo, M.C. 2004. The ecology of large herbivores in the Okavango Delta, Botswana. PhD thesis - University of Bristol, UK.

## References

---

- Boyd, L. & Keiper, R. 2005. Behavioral ecology of feral horses. In: *The Domestic Horse: The Origins, Development, and Management of its Behaviour*, ed. D.S. Mills & S.M. McDonnell. Cambridge University Press, pp. 55-82.
- Brooks, C.J. 2005. The foraging behaviour of Burchell's zebra (*Equus burchelli antiquorum*). University of Bristol, pp 232
- Burnham, K.P. & Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. *Wildlife 2001: Populations* (eds D.R. McCullough & R.H. Barrett), pp. 16–30. Elsevier. Science Publishers, London, England.
- Burnham, K.P. & Anderson, D.R. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer Verlag, Berlin.
- Cabrera, A. 1936. Subspecific and individual variation in the Burchell zebras. *Journal of Mammalogy* 17:89-112
- Cameron, E. Z. & Linklater, W. L. 2000. Individual mares bias investment in sons and daughters in relation to their condition . *Animal Behaviour* 60, 359-367.
- Cameron, E. Z., Linklater, W. L., Minot, E. O., & Stafford, K. J. 2001, Population dynamics 1994-98, and management of Kaimanawa wild horses, Department of Conservation, Wellington, New Zealand.
- Caro, T. M. 1999. Densities of mammals in partially protected areas: the Katavi ecosystem of western Tanzania. - *Journal of Applied Ecology* 36: 205-217.
- Caswell, H. 1978. Predator - mediated coexistence: a nonequilibrium model. *American Naturalist* 112:127-154
- Caswell, H. 2001. *Matrix population models. Construction, analysis and interpretation*. Second Edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.
- Catchpole, E.A., Morgan, B.J.T., Coulson, T.N., Freeman, S.N. & Albon, S.D. 2000. Factors influencing Soay Sheep survival. *Applied Statistics* 49:453-472
- Catchpole, E.A., Fan, Y., Morgan, B.J.T., Clutton-Brock, T.H. & Coulson, T. 2004. Sexual dimorphism, survival and dispersal in red deer. *Journal of Agricultural, Biological, and Environmental Statistics* 9:1-26
- Caughley, G. 1977. *Analysis of vertebrate populations*. Wiley & Sons, New York
- Caughley, G., Birch, L.C. 1971. Rate of increase. *Journal of Wildlife Management* 35:658-663
- Chamaillé-Jammes, S., Fritz, H., Murindagomo, F. In press. Spatial patterns of the NDVI – rainfall relationship at the seasonal and interannual time – scales in an African savanna. *International Journal of Remote Sensing*.
- Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA.
- Child, G., Robbel, H. and Hepburn, C. P. 1972. Observations on the biology of tsessebe, *Damaliscus lunatus lunatus*, in northern Botswana. - *Mammalia* 36: 342-388.
- Choquet, R., Reboulet, A.M., Pradel, R., Gimenez, O. & Lebreton, J.D. 2005a. M-SURGE 1.7 User's Manual. CEFE, Montpellier, France. (<http://ftp.cefe.cnrs.fr/biom/Soft-CR/>)

- Choquet, R., Reboulet, A.M., Lebreton, J.D., Gimenez, O. & Pradel, R. 2005b. U-CARE 2.2 User's Manual. CEFE, Montpellier, France. (<http://ftp.cefe.cnrs.fr/biom/Soft-CR/>)
- Clutton-Brock, T.H. & Coulson, T. 2002. Comparative ungulate population dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society, London B* 357:1285-1298
- Coe, M.J., Cumming, D.H., Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22:341-354
- Cooper, S.M. 1990. The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. *African Journal of Ecology* 28:131-141
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. 2001. Age, sex, density, winter weather, and population crashes in Soay Sheep. *Science* 292:1528-1531
- Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429-438
- Crawley, M. J. 2002. *Statistical computing: An introduction to data analysis using S-Plus*. – John Wiley & Sons Ltd, Chichester, UK.
- Cumming, D. H. M. 1982. The influence of large herbivores on savanna structure in Africa. - In: Huntley, B. J. and Walker, B. H. (eds.), *Ecology of Tropical Savannas*. Springer Verlag, pp. 217-244.
- Danell, K., Bergstrom, R., Duncan, P. & Pastor, J. 2006. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* Cambridge University Press
- De Boer, W., & Prins, H. 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82:264-274
- Donlan, J., Greene, H. W., Berger, J., Bock, C. E., Bock, J. H., Burney, D. A., Estes, J. A., Foreman, D., Martin, P. S., Roemer, G. W., Smith, F. A., & Soulé, M. E. 2005. Re-wilding North America. *Nature* 436, 913-914.
- Douglas-Hamilton, I. 1972. On the ecology and behavior of the African elephant: the elephants of Lake Manyara. D. Phil. Thesis, Oxford University
- Drouet-Hoguet N. 2005. Research for management of African protected areas, experience from research in Hwange National Park. – Hwange workshop, 14-21 November 2005, Jwapi Lodge, Zimbabwe.
- Du Toit, J. T., Rogers, K. H. and Biggs, H. C. 2003. *The Kruger Experience: ecology and management of savanna heterogeneity*. - Island Press, Washington.
- Dublin, H. T., Sinclair, A. R. E., Boutin, S., Anderson, E., Jago, M. and Arcese, P. 1990. Does competition regulate ungulate populations ? Further evidence from Serengeti, Tanzania. - *Oecologia* 82: 283-288.
- Duncan, P. 1982. Foal killing by stallions. *Applied Animal Ethology* 8:567-570.
- Duncan, P. 1992a. Zebras, Asses and Horses. An action plan for the conservation of wild equids. IUCN/SSC Equid Specialist Group. pp. vii + 37

- Duncan, P. 1992b. *Horses and Grasses: The nutritional ecology of Equids and their impact on the Camargue* Springer-Verlag Inc., New York.
- Duncan, P., Harvey, P.H. & Wells, S.M. 1984. On lactation and associated behaviour in a natural herd of horses. *Animal Behaviour* 32:255–263.
- Duncan, P., Foose, T. J., Gordon, I., Gakahu, C. G. and Lloyd, M. 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. - *Oecologia* 84: 411-418.
- East, R. 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. - *African Journal of Ecology* 22: 245-270.
- East, R. 1996a. Antelope Survey Update. Number 2: September 1996 - IUCN/SSC Antelope Specialist Group Report.
- East, R. 1996b. Antelope Survey Update. Number 3: December 1996 - IUCN/SSC Antelope Specialist Group Report.
- East, R. 1997a. Antelope Survey Update. Number 4: February 1997 - IUCN/SSC Antelope Specialist Group Report.
- East, R. 1997b. Antelope Survey Update. Number 2: June 1997 - IUCN/SSC Antelope Specialist Group Report.
- East, R. 1997c. Current status of Burchell's zebra in Africa. With additional information on Grevy's zebra and Cape Mountain zebra. IUCN/SSC and Equid Specialist Group.
- East, R. 1999. African Antelope Database 1998. - IUCN/SSC Antelope Specialist Group, IUCN. 444 pp.
- Eberhardt, L. L. 1977. Optimal policies for the conservation of large mammals, with special reference to marine ecosystems. *Environmental Conservation* 4:205–212.
- Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83, 2841-2854.
- Estes, R.D. 1991. *The behaviour guide of African mammals*. The University of California Press, Berkeley and Los Angeles, California
- Festa-Bianchet, M., Gaillard, J.M., Coté, S.D. 2003. Variable age structure and apparent density-dependence in survival of adult ungulates. *Journal Animal Ecology* 72:640–649
- Fritz, H. and Duncan, P. 1994. On the carrying capacity for large ungulates of African savanna ecosystem. – *Proceedings of the Royal Society London B* 256: 77-82.
- Fryxell, J., Greever, J., Sinclair, A. 1988. Why are migratory ungulates so abundant? *American Naturalist* 131:781–798
- Fryxell, J.M, Sinclair, A.R.E. 1988. Seasonal migration by white-eared kob in relation to resources. *African Journal of Ecology* 26:17–31

## References

---

- Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G., Boisaubert, B. & Pradel, R. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. *Journal of Animal Ecology*, 62, 778–791.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58–63
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toïgo, C. 2000a. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31, 367-393.
- Gaillard, J.-M., Festa-Bianchet, M., Delorme, D., & Jorgenson, J. 2000b. Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society, London B* 267, 471-477.
- Garrott, R. A. & Taylor, L. 1990. Dynamics of a feral horse population in Montana. *Journal of Wildlife Management* 54, 603-612.
- Garrott, R.A., Siniff, D.B., Eberhardt, L.L. 1991. Growth rates of feral horse populations. *Journal of Wildlife Management* 55:641-648
- Gasaway, W. C., Gasaway, K. T. and Berry, H. H. 1996. Persistent low densities of plains ungulates in Etosha National Park, Namibia: testing the food-regulating hypothesis. – *Canadian Journal of Zoology* 74: 1556-1572.
- Georgiadis, N., Hack, M. and Turpin, K. 2003. The influence of rainfall on zebra population dynamics: implications for management. - *Journal of Applied Ecology* 40: 125-136.
- Gordon, I.J., Duncan, P., Grillas, P., Lecomte, T. 1990. The use of domestic herbivores in the conservation of the biological richness of European wetlands. *Bulletin d'Ecologie* 21:49-60
- Grange, S., Duncan, P., Gaillard, J.-M., Sinclair, A. R. E., Gogan, P. J. P., Packer, C., Hofer, H. and East, M. 2004. What limits the Serengeti zebra population? - *Oecologia* 140: 523-532.
- Grimsdell, J.J.R. 1973. Age determination of the African buffalo, *Syncerus caffer* Sparrman. *East African Wildlife Journal* 11:31–54
- Gross, J. E. 2000. A dynamic simulation model for evaluating effects of removal and contraception on genetic variation and demography of Pryor Mountain wild horses. *Biological Conservation* 96, 319-330.
- Groves, C.P. 1974. Horses, asses and zebras in the wild. David and Charles, Newton Abbot, London
- Groves, C.P., Bell, C.H. 2004. New investigations on the taxonomy of the zebras genus *Equus*, subgenus *Hippotigris*. *Mammalian Biology* 69:182-196
- Gwynne, M.D., Bell, R.H.V. 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* 220:390-393
- Hack, M.A., East, R., Rubenstein, D.I. 2002. Status and action plan for the Plains zebra (*Equus burchellii*). In: Moehlman P. (ed.) *Equids: Zebras, Asses and Horses. Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland and Cambridge, UK, IUCN/SSC Equid Specialist Group, pp. 43-60.

## References

---

- Hairston, N.G., Smith, F.E., Slobotkin, L.B. 1960. Community structure, population control, and competition. *American Naturalist* 44:421-425
- Hall, S.J.G., Hall, J.G. 1988. Inbreeding and population dynamics of the Chillingham cattle. *Journal of Zoology* 216:479-493
- Hansen, R.M., Mugambi, M.M., Bauni, S.M. 1985. Diets and trophic ranking of ungulates of the northern Serengeti. *Journal of Wildlife Management* 49:823-829
- Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R., Funston, P. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation* 90:69-78.
- Hennecke, D.R., Potter, G.D., Kreider, J.L. 1981. A condition score relationship to body fat content of mares during gestation and lactation. pp. 105-110. In *Proceedings of the 7<sup>th</sup> Equine Nutrition Physiology Symposium*
- Henschel, J.R. 1986. The socio-ecology of spotted hyena *Crocuta crocuta* clan in the Kruger National Park. - D.Sc. thesis, University of Pretoria.
- Hillman, J. C. and Hillman, A. K. K. 1977. Mortality of wildlife in Nairobi National Park, during the drought of 1973-1974. - *East African Wildlife Journal* 15: 1-18.
- Hofer, H., East, M.L. 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. I- Social organization. *Animal Behaviour* 46:547-557
- Hofer, H. and East, M. 1995. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. - In: Sinclair, A. R. E. and Arcese, P. (eds.), *Serengeti II: Dynamics, management, and conservation of an ecosystem*. The University of Chicago Press, pp. 332-363.
- Hofer, H., Campbell, K.L.I., East, M.L., Huish, S.A. 1996. The impact of game meat hunting on target and non-target species in the Serengeti. In: Taylor V., Dunstone N. (eds) *The exploitation of mammal populations*. Chapman and Hall, London, pp 117-146
- Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443-457
- Janis, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* 30:757-774
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-247
- Jolly, G.M. 1969. The treatment of errors in aerial counts of wildlife populations. *East African Agricultural and Forestry Journal* 34:50-55
- Jolly, G.M. 1982. Mark-recapture models with parameters constant in time. *Biometrics* 38:301-321
- Joubert, E. 1972. The social organization and associated behaviour in the Hartmann zebra (*Equus zebra hartmannae*). *Madoqua Series I*, 6:17-56.
- Kampf, H. 2000. The role of large grazing animals in nature conservation - a Dutch perspective. *British Wildlife* 12:1-10

## References

---

- Kingdon, J. 1982. East African Mammals. An Atlas of Evolution in Africa. Vol. III C. Bovids. - London Academic Press.
- Kissui, B. M. and Packer, C. 2004. Top-down population regulation of a top predator: lions in the Ngorongoro Crater. - Proceedings of the Royal Society London B 271: 1867-1874.
- Klingel, H. 1967. Soziale organisation und Verhalten freilebender Steppenzebras. Zeitschrift für Tierpsychologie 24:580-624
- Klingel, H. 1969a. The social organization and population ecology of the Plains zebra (*Equus quagga*). Zoologica Africana 4:249-263
- Klingel, H. 1969b. Reproduction in the Plains zebra, *Equus burchelli boehmi*: Behaviour and ecological factors. Journal of Reproduction and Fertility Supplement 6:339-345
- Klingel, H. 1974. A comparison of the social behaviour of Equidae. In: Geist V, Walter F (eds) The Behaviour of Ungulates and its Relation to Management - vol.1 International Union for the Conservation of Nature and Natural Resources, Morges, pp 124-132
- Klingel, H. 1982. Social organization of feral horses. Journal of Reproduction and Fertility, 32:89-95
- Kruuk, H. 1972. The spotted hyena: a study of predation and social behaviour. University of Chicago Press, Chicago.
- Lebreton, J.D., Millier, C. 1982. Modèles dynamiques déterministes en biologie. Masson, Paris, pp. 208
- Lebreton, J-D., Burnham, K.P., Clobert, J., Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118
- Legendre, S., Clobert, J. 1995. ULM, a software for conservation and evolutionary biologists. Journal of Applied Statistics 22:817-834
- Leslie, P.H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria Aalge Pont.*). Journal of Animal Ecology 35:291-301
- Loison, A., Festa-Bianchet, M., Gaillard, J.M., Jorgenson, J.T., Jullien, J.M. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539-2554
- Lotka, A.J. 1925. Elements of physical biology. Baltimore: Williams and Wilkins
- Mac Arthur, R.H., Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101:377-385
- Maddock, L. 1979. The "Migration" and Grazing Succession. In: Sinclair ARE, Norton-Griffiths M (eds) Serengeti: Dynamics of an Ecosystem The University of Chicago Press, Chicago and London, pp 104-129
- Malthus, T.R. 1798. An essay on the principle of population. London: J. Johnson
- Mason, D.R. 1985. Postnatal growth and physical condition of warthogs *Phacochoerus aethiopicus* in Zululand. - South African Journal of Wildlife Research 15: 89-97.
- May, R.M. 1975. Some notes on estimating the competition matrix a. Ecology 56:737-741

- Mduma, S. A. R., Sinclair, A. R. E. and Hilborn, R. 1999. Food regulates the Serengeti wildebeest: a 40-year record. - *Journal of Animal Ecology* 68: 1101-1122.
- Mech, L. D. 1970. *The wolf: the ecology and behavior of an endangered species*. - Doubleday Publishing Co., New York.
- Ménard, C., Duncan, P., Fleurance, G., Georges, J.-Y. and Lila, M. 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. - *Journal of Applied Ecology* 39: 120-133.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. - *Ecology* 75: 478-488.
- Mills, M.G.L. and Shenk, T.M. 1992. Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology* 61:693-702
- Mills, M.G.L., Biggs, H.C., Whyte, I.J. 1995. The relationship between rainfall, lion predation and population trends in African herbivores. *Wildlife Research* 22:75-88
- Mills, M.G.L. and Hofer, H. 1998. *Hyaenas. Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland and Cambridge, UK, IUCN/SSC Hyaena Specialist Group, pp. 154
- Moehlman, P.D. 2002. *Equids: Zebras, Asses and Horses. Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland and Cambridge, UK, IUCN/SSC Equid Specialist Group, pp. 190
- Monfort, A., Monfort, N. 1978. Structure et répartition des populations de zèbres (*Equus burchelli*) du Parc de l'Akagera (Rwanda). *Mammalia* 42:315-322
- Ogutu, J.O., Owen-Smith, N. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters* 6:412-419
- Ogutu, J.O., Owen-Smith, N. 2005. Oscillations in large mammal populations: are they related to predation or rainfall? *African Journal of Ecology* 43:332-339
- Olf, H., Brown, V.K. & Drent, R.H. 1999. *Herbivores: Between Plants and Predators*. Blackwell Science. pp x+639.
- Owen-Smith, N. 1988. *Megaherbivores: the influence of very large body size on ecology*. - Cambridge University Press.
- Owen-Smith, N. 1990. Demography of a large herbivore, the greater Kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology* 59:893-913
- Owen-Smith, N., Mason, D.R. 2005. Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. *Journal of Animal Ecology* 74:762-773
- Owen-Smith, N., Mason, D.R. and Ogutu, J.O. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. - *Journal of Animal Ecology* 74: 774-788.
- Packer, C., Scheel, D., Pusey, A.E. 1990. Why lions form groups: food is not enough. *American Naturalist* 136:1-19
- Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science* 307:390-393

- Penzhorn, B. L. 1984. A long-term study of social organisation and behavior of Cape mountain zebra *Equus zebra zebra*. *Zeitschrift für Tierpsychologie*, 64 :97-146.
- Petersen, J.C.B. 1972. An identification system for zebra (*Equus burchelli*, Gray). *East African Wildlife Journal* 10:59-63
- Pienaar, U. de V. 1963. The large mammals of the Kruger National Park. Their distribution and present-day status. *Koedoe* 6:1-37
- Pienaar, U. de V. 1969. Observations on development biology, growth and some aspects of the population ecology of African buffalo in the Kruger National Park. - *Koedoe* 12: 29-52.
- Pluhacek, J. and Bartos, L. 2000. Male infanticide in captive plains zebra, *Equus burchelli*. - *Animal Behaviour* 59: 689-694.
- Pluhacek, J., Bartos, L., Vichova, J. 2006. Variation in incidence of male infanticide within subspecies of Plains zebra (*Equus burchelli*). *Journal of Mammalogy* 87: 35-40.
- Prins, H.H.T. 1996. Behaviour and ecology of the African buffalo: social inequality and decision making. Chapman and Hall, London
- Prins, H. H. T. and Douglas-Hamilton, I. 1990. Stability in a multi-species assemblage of large herbivores in East Africa. - *Oecologia* 83: 392-400.
- Pusey, A. and Packer, C. 1987. Philopatry and dispersal in lions. - *Behaviour* 101: 275-310.
- Redfern, J. V., Grant, R., Biggs, H. C. and Getz, W. M. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. - *Ecology* 84: 2092-2107.
- Redfern, J. V., Ryan, S. J. and Getz, W. M. 2006. Defining herbivore assemblages in the Kruger National Park: a correlative coherence approach. - *Oecologia* 146: 632-640.
- Rikoon, J.S. 2006. Wild horses and the political ecology of nature restoration in the Missouri Ozarks. *Geoforum* 37:200-211
- Rosenzweig, M. 1996. Species diversity in space and time. Cambridge University Press, Cambridge
- Rosser, A. M. 1987. Resource defence in an African antelope, the puku (*Kobus vardoni*). - Ph.D. thesis, University of Cambridge.
- Rubenstein, D.I. 1986. Ecology and Sociality in Horses and Zebras. In: Rubenstein DI, Wrangham RW (eds) *Ecological Aspects of Social Evolution. Birds and Mammals* Princeton University Press, Princeton, New Jersey, pp 282-302
- Ryder, O. 1990. Putting the wild horse back into the wild. In: Przewalski's Horse Global Conservation Plan. Zoological Society of San Diego, Center for Reproduction of Endangered Species.
- Ryder, O. A. & Massena, R. 1988. A case of male infanticide in *Equus przewalskii*. *Applied Animal Behaviour Science*, 21:187-190.
- Sachs, R. 1967. Liveweights and body measurements of Serengeti game animals. - *East African Wildlife Journal* 5: 24-36.
- Schaller, G.B. 1972. The Serengeti lion. The University of Chicago Press, Chicago

- Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, USA
- Seddon, P.J., Soorae, P.S. 1999. Guidelines for subspecific substitutions in wildlife restoration projects. *Conservation Biology* 13:177-184
- Sinclair, A.R.E. 1974. The natural regulation of buffalo populations in East Africa. IV. The food supply as a regulating factor, and competition. *East African Wildlife Journal* 12:291-311
- Sinclair, A.R.E. 1977. The African buffalo. A study of resource limitation of populations. - The University of Chicago Press, Chicago & London.
- Sinclair, A.R.E. 1985. Does interspecific competition or predation shape the African ungulate communities? *Journal of Animal Ecology* 54:899-918
- Sinclair, A.R.E. 1989. Population regulation in animals. In: Cherret JM (ed). *Ecological concepts: the contribution of ecology to an understanding of the natural world* Blackwell Scientific Publications, Oxford, pp 197-241
- Sinclair, A.R.E. 1997. Fertility control of mammal pests and the conservation of endangered marsupials. *Reproduction, Fertility and Development* 9:1-16
- Sinclair, A.R.E. & Norton-Griffiths, M. 1979. *Serengeti: Dynamics of an ecosystem*. - The University of Chicago Press Chicago.
- Sinclair, A.R.E., Norton-Griffiths, M. 1982. Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. *Oecologia* 53:364-369
- Sinclair, A.R.E., Dublin, H.T., Borner, M. 1985. Population regulation of Serengeti wildebeest: a test of the food hypothesis. *Oecologia* 65:266-268
- Sinclair, A.R.E. & Arcese, P. 1995. *Serengeti II: Dynamics, management, and conservation of an ecosystem*. - The University of Chicago Press.
- Sinclair, A.R.E., Mduma, S.A.R., Arcese, P. 2000. What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology* 81:2100-2111
- Sinclair, A.R.E., Krebs, C.J. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society, London B* 357:1221-1231
- Sinclair, A.R.E., Fryxell, J.M. & Caughley, G. 2006. *Wildlife ecology, conservation, and management*. Second Edition. Blackwell Publishing Ltd, Oxford. 469 pp.
- Skinner, J. D. 1980. Productivity of mountain reedbuck, *Redunca fulvorufula* (Afzelius, 1815) at the Mountain Zebra National Park. - *Koedoe* 23: 123-130.
- Skinner, J.D., Smithers, R.H.N. 1990. *The mammals of the Southern African Subregion*. University of Pretoria, Pretoria, Republic of South Africa
- Skoog, R.O., Gogan, P.J.P. 1970. Population ecology of the plains zebra in the Serengeti-Mara ecosystem (progress reports n°1 & 2).

- Smithers, R. H. N. 1971. The Mammals of Botswana. - Salisbury: Trustees of the National Museums of Rhodesia.
- Smithers, R. H. N. & Wilson, V. J. 1979. Check list and atlas of the mammals of Zimbabwe Rhodesia. – Memorial of the National Museums and Monuments of Rhodesia 9: 1-147.
- Smuts, G.L. 1975. Pre- and post-natal growth phenomena of Burchell's zebra from the Kruger National Park. - Koedoe 18: 69-102.
- Smuts, G.L. 1976a. Reproduction in the zebra mare *Equus burchelli antiquorum* from the Kruger National Park. Koedoe 19:89-132
- Smuts, G.L. 1976b. Population characteristics of Burchell's zebra (*Equus burchelli antiquorum*, H.Smith, 1841) in the Kruger National Park. South African Journal of Wildlife Research 6:99-112
- Smuts, G.L. 1978. Interrelations between predators, prey, and their environment. BioScience 28:316–320
- Smuts, G.L. 1982. Lion. - Macmillan, Johannesburg.
- Solberg, E.J., Grotan, V., Rolandsen, C.M., Broseth, H. & Brainerd, S. 2005. Change-in-sex ratio as an estimator of population size for Norwegian moose *Alces alces*. Wildlife Biology 11, 163-172.
- Spinage, C.A. 1972. African ungulate life tables. Ecology 53:645-652
- Tello, J. L. P. L. and van Gelder, R. G. 1975. The natural history of nyala, *Tragelaphus angasi* (Mammalia, Bovidae) in Mozambique. - Bulletin of the American Museum of Natural History 155: 323-385.
- The R Development Core Team. 2004. R: A Language and Environment for Statistical Computing. Version 2.0.1 (2004-11-15). Copyright (©) 1999–2003. R Foundation for Statistical Computing
- Tokeshi, M. 1999. Species coexistence: Ecological and Evolutionary Perspectives. Blackwell Science, Oxford, pp. 454
- Treisman, M. 1975. Predation and the evolution of gregariousness. I. Models for concealment and evasion. Animal Behaviour 23:779–800
- Twine, W. 2002. Feeding time budgets of selected African ruminant and non-ruminant grazers. African Journal of Ecology 40:410-412
- Van Dierendonck, M. C. & Wallis de Vries, M. F. 1996. Ungulate Reintroductions: Experiences with the Takhi or Przewalski Horse (*Equus ferus przewalskii*) in Mongolia. Conservation Biology 10, 728-740.
- Van Wieren, S.E. 1996. Digestive strategies in ruminants and nonruminants. PhD thesis. Agricultural University, Wageningen
- Verhulst, P.F. 1838. Notice sur la loi que la population suit dans son accroissement. Corresp. Math. Phys. A. Quetelet 10: 113-121
- Vesey-Fitzgerald, D. 1960. Grazing succession amongst East African game animals. Journal of Mammalogy 41:161-170

## References

---

- Viljoen, P. C. 1982. Die gedragsekologie van die oorbietjie *Ourebia ourebi ourebi* (Zimmerman, 1783) in Transvaal. - M.Sc. Thesis. University of Pretoria.
- Volterra, V. 1926. Variations and fluctuations of the number of individuals in animal species living together. In *Animal Ecology*, ed. R.N. Chapman (ed.), New York: McGraw-Hill, pp 409-448
- Vulink, J. T. 2001. Hungry herds. Management of temperate lowland wetlands by grazing. PhD thesis - University of Groningen, The Netherlands.
- Watson, R.M. 1967. The population ecology of the Serengeti wildebeest. PhD thesis. Cambridge University, Cambridge
- Watson, R.M. 1969. Reproduction of wildebeest, *Connochaetes taurinus albojubatus* Thomas, in the Serengeti region, and its significance to conservation. *Journal of Reproduction and Fertility* [Supplement] 6:287-310
- Welsh, D. A. 1975, Population, behavioural and grazing ecology of the horses of Sable Island, Nova Scotia, Dalharsic University.
- Willmott, C. J. and Matsuura, K. 1998. Global air temperature and precipitation: regridded monthly and annual climatologies (Version 2.01). Available on-line at [<http://climate.geog.udel.edu/~climate>] from the Center for Climatic Research, Department of Geography, University of Delaware, Newark, Delaware, USA.
- Wilson, V. J. 1966. Observations on Lichtenstein's haterbeest, *Alcelaphus lichtensteini*, over a three-year period, and their response to various tsetse control measures in Eastern Zambia. - *Arnoldia Rhodesia* 2: 1-13.
- Wilson, V. J. 1970. Data from the culling of kudu, *Tragelaphus strepsiceros*, in the Kyle National Park. - *Arnoldia Rhodesia* 4: 1-26.
- Wilson, V. 1997. Biodiversity of Hwange National Park. Large mammals and carnivores. Chipangali Wildlife Trust, Harare.



## **Abstract**

The plains zebra is currently the most widespread wild equid; however there is still little information on the regulation/limitation of their populations. Comparative studies on the relative abundance and the population dynamics of plains zebras and grazing bovids support the hypothesis that predation has a greater impact on the number of zebras in African ecosystems, and probably also play an important role in the limitation of some zebra populations. Given these findings, it will be necessary to link population models of zebra and their main predators. However a major problem is the lack of accurate data on zebra survival rates. The study on the population dynamics of plains zebra in Hwange National Park (Zimbabwe) is the first one to use a capture-mark-recapture method based on photo-identification. After only one year and a half, this method already proves to be promising to study zebra population dynamics. This thesis also shows that the feralization of domestic horses leads to an unnatural population dynamics, which means that Camargue horses cannot be used as surrogates of wild equids to restore natural ecosystems. In terms of species conservation it is therefore now important to acquire a good knowledge on the regulating/limiting factors acting on current wild equid populations in order to facilitate translocations and reintroductions in their natural ecosystems.

## **Discipline**

Physiology, animal biology, populations, interactions

## **Keywords**

Coexistence, equids, population dynamics, predation, regulation / limitation, zebra

**Centre d'Etudes Biologiques de Chizé, CNRS, UPR 1934, 79360 Beauvoir-sur-Niort, FRANCE**