Order Number 9237216

Mother-infant behavior and ecology of Grevy's zebra, *Equus grevyi*

Rowen, Mary, D.F.

Yale University, School of Forestry and Environmental Studies, 1992

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

Mother-infant Behavior and Ecology of Grevy's Zebra *Equus grevyi*

A Dissertation
Presented to the Faculty of the
School of Forestry and Environmental Studies
Yale University
in Candidacy for the Degree of
Doctor of Forestry and Environmental Studies

by
Mary Rowen

May, 1992

YALE UNIVERSITY SCHOOL OF FORESTRY AND ENVIRONMENTAL STUDIES

NOTICE OF DOCTOR OF FORESTRY DISSERTATION SUBMITTED TO THE REGISTRAR'S OFFICE

Student: MARY ROWEN

Department: F&ES

Date Submitted: May 18, 1992

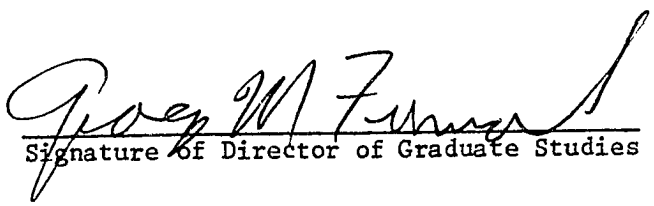
Dissertation Director: William R. Burch

Dissertation Title: Mother-infant behavior and ecology of Grevy's Zebra, *Equus grevyi*

Please list all readers below, their exact titles and addresses, and return to the Registrar's Office as soon as possible.

We must have SOCIAL SECURITY NUMBERS for ALL OUTSIDE READERS. Please indicate whether or not a copy of the dissertation should be sent to outside readers.

Name	Title	Address	Send Copy to outside reader
Daniel I. Rubenstein	Professor	Princeton University Dept. of Ecology and Evolutionary Biology Eno Hall Princeton, NJ 08544-1003	YES
Alison F. Richard	Professor	Anthropology & Environmental Studies 51 Hillhouse	
Patricia D. Moehlman	Senior Research Assoc.	Wildlife Conservation International New York Zoological Society Bronx Zoo Bronx, NY 10460	



Signature of Director of Graduate Studies

May 25, 1992

Date

ABSTRACT

Mother-infant Behavior and Ecology of
Grevy's Zebra, *Equus grevyi*

Mary Rowen
School of Forestry and Environmental Studies
Yale University
1992

Mother-infant behavior of Grevy's zebra (*Equus grevyi*) is analyzed in relation to parental investment, infant survival and the function of mother-infant groups. Behavioral and ecological data were collected on 1,000+ individually recognized zebra in Buffalo Springs, Samburu and Shaba National Reserves, Kenya.

Maternal input, in terms of milk allocation, was similar for male and female infants throughout early and midlactation (0-6 months). Male and female infants used similar behaviors to initiate suckling; at the same time, lactating females used similar levels of aggression to terminate male and female suckling bouts. Comparison with previous work on this species indicates that while suckling time varies with environmental conditions, maternal input is equal for male and female infants.

Mothers and infants within the reserves tended to stay on fewer than two male territories during early and mid lactation. Within the study area, mother-infant pairs that remained in one area experienced lower infant mortality compared to mother-infant pairs that moved in and out of the

reserves on a regular basis. Before they began drinking water on their own at four months, foals outside the reserves suffered 3-5 times greater mortality than foals in stable groups within the reserves.

Infants in groups participated in social play similar to that seen in harem social systems. Territorial stallions did not interact with infants on a regular basis. Stallion chases of foals were rare and appeared to be a method for moving adult females across territory boundaries rather than attempts to injure infants.

Conservation plans for this species must ensure maintenance of major foaling areas. Tourist and pastoralist use of certain important water sources must be monitored such that their use does not decrease the survivorship of young Grevy's zebra foals.

ACKNOWLEDGEMENTS

I am very grateful to the Government of Kenya for allowing me to conduct my research in Kenya. I thank The Office of the President, the National Research Council of the Ministry of Science and Technology, and the Kenyan Wildlife Service (KWS) for granting permission to study within the Buffalo Springs, Samburu and Shaba National Reserves. I am grateful for the help and assistance of Dr. David Andere and his staff, of the Department of Resource Surveys and Remote Sensing, both for sponsoring my research and for the many discussions regarding arid-land ecology.

I would like to thank the County Councils of both Samburu and Northeastern districts for allowing me access to their reserves. Perez Olindo kindly introduced me to the wardens at the Buffalo Springs Shaba and Samburu areas. For helping me get started and for our many conversations, I am grateful. I extend special thanks to the wardens, rangers, and staff of the Buffalo Springs, Samburu and Shaba National Reserves. Without their friendship and assistance this project would not have been possible. I am indebted to KWS Warden Gilbert Irangi, and Assistant Wardens Abdulkadir Biru, Dominic Miana and Wiachera for their unending support and friendship. From them I learned about wildlife and reserve management, and various issues concerning the

pastoral peoples who share their land with wildlife. Special thanks to Dominic and Clemens Miana for including me in their home on many special occasions. Thanks to Abdulkadir Biru, Mohammed Bidu and Abdi Boro for new card games and shared dinners. I am very grateful to A. Biru and G. Irangi for the many game drives where I saw and learned much about non-equine matters.

Many and heartfelt thanks to those who provided funding for this project. The Tropical Resources Institute, Yale University provided initial monies to start the project. Mr. William Gruenerwald graciously extended permission and support for an initial study at the Canyon Colorado Equid Sanctuary. My work there enabled me to start my project galloping once I arrived in Kenya, and for that I cannot sufficiently thank him. I am grateful to the SEACON committee of the Chicago Zoological Society that provided the majority of support for this project. Many people at Chicago Zoological Society have aided me in numerous ways over the years; thanks are extended to Pam Parker, Ann Petric, Mary and George Rabb, and Lou and Nancy Schauer. I would especially like to thank George Rabb for giving me the opportunity to learn about conservation and animal behavior. On looking back, I see how my progress down the path has received gentle prodding from him from time to time. Thanks.

Simple thanks for my committee are not enough. I am very grateful to Patricia Moehlman for accepting the project

and for her help in regard to background information, sampling techniques and logistical support. Both in the field and while writing, Patti has been a friend and a mentor - at all times asking questions, sharing ideas and providing support; for her advice and good humor I thank her.

After Patti left for East Africa, William Burch Jr. gallantly stepped in as my committee chair and has, without complaint, seen the project to completion. In addition, Bill has provided me with insight as to the role of Grevy's zebra in the greater scheme of things; Bill has the ability to see, digest and draw parallels with matter outside his own extensive bookshelves, and for this I thank him. Alison Richard has, at every step of the way, provided insight and support. She has the rare ability to juggle many different types of activities while being able to focus clearly on the issue at hand. I have profited greatly from our discussions of social behavior and parental care. I am very grateful to Steve Beissinger for joining the project. This project has benefitted from the fact that Steve's door was always open for help and discussion. Our discussions were very useful in making me hone and reformulate my ideas. For his unstinted help and support, thanks.

Early discussions with Dan Rubenstein helped formulate ideas and questions. When called upon, he has generously shared ideas and cheered the process forward; both behaviors

have been greatly appreciated.

Special and heartfelt thanks to Josh Ginsberg who agreed, during that territorial period of writing his own thesis on this species, to help me get started on my own project. Josh taught me how to identify the critters and provided me with maps and grids of Buffalo Springs and Samburu reserves. With his help I was able to start taking data almost immediately. For the above and for his friendship, ideas, support and understanding I am indebted.

Such projects as this are not completed without a good deal of generosity on the part of strangers, acquaintances and good friends. Liz Bear, Bjorn Figenschou, and Pat and Bob Jaeger provided support and friendship, and, best of all, never asked difficult questions. Debbie and Don Conner, and Geu and Fredrique Grootenhuis graciously shared dinners and provided logistical support. At Yale, Doreen Corcoran, Nancy Rabbott and Ann Ramadei have always known the answers that others did not.

Discussions with Dusty Becker, Tim Clark, Patrick Duncan, Kathy Freas, and Dorcas MacClintock have been very helpful in the gestation of this dissertation. Discussions with Cris Field, Hugh Lamprey, Mike Rainy, and Mark Stanley-Price were very helpful in learning some of the specifics of the northern areas. I am grateful to Mark Stanley-Price, Debbie Snelson and the rest of the AWF crew in Nairobi for making me welcome. Many thanks to the Craig family for

their hospitality and for allowing me to photograph the Grevy's zebra on their land.

Thanks to Tom and Wahida Plummer, Nina Marshall, Jared Crawford, and Hilary and John Morland for allowing me to stay in their homes during my forays into Nairobi. Discussions and dinners with them and with Marion East, Jess Grunblat, Heribert Hofer, Mirka Prazak, Robert Pini, and Gary Tabor made my visits to Nairobi both a culinary and intellectual treat. Within the reserves, the managers and staff of the Samburu/Larsen's lodges, Serena Lodge and, in particular, Buffalo Springs lodge were extremely helpful in providing logistical and mechanical support. For their help and friendship, thanks.

In New Haven, I have seen many students wander in and out of the school. I would like to thank Jean Brennan, Peyton Curlee, Liz Kramer, Peter Schyler, Lili Sheeline, Gary Tabor and many others for their friendship and support during various stages of this dissertation. On a more permanent basis, I have shared the joys, frustrations and hours of "well at my field site...." stories with my fellow doctoral students. Sharing thesis life with Nora Bynum, Rich Carrol, Jock Conyngham, James Gibbs, Rich Reading, Vasant Saberwal, Whendee Silver-Beissinger, Katherine Snyder, Eleanor Sterling, Scott Stoleson, Sarah Warren and Andy Young has added many new laugh lines and has increased my knowledge of many little known facts.

The last few months would not have been possible without several fellow thesis writers - thanks to Nora Bynum for all her good sense and support, especially at crunch times; Eleanor Sterling, with whom tangential discussions are a delight; and Sarah Warren who has allowed me to spread my belongings over our palatial office and has provided friendship and support under trying conditions.

I thank James Gibbs and Larry Gall for their statistical help and for knowing what I meant when articulation was beyond me. Special thanks to Charles Brown both for early discussions of this project and for analyzing the mark-resighting data using SURGE on his computer. I am indebted to Denise Casey for her help on the maps.

To my family and friends, thanks for your support and for not asking "are you done?" too often.

As the second Grevy's zebra researcher to grow up in the heart of New York City, I too would like to thank my family for instilling in me a sense of value, love and interest in natural environments. Early in life my brothers taught me lessons in Darwinian survival. More recently they have provided friendship and encouragement; for both I am deeply appreciative. I think that the idea of another child in the family trade drove my parents to support my interest in natural sciences with exuberance. For their sense of humor, friendship, love and support, thanks.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION, STUDY AREA, AND ANIMAL IDENTIFICATION

INTRODUCTION

Ultimately, the success of a species depends on its ability to produce viable offspring that in turn reproduce. The length of post-copulatory investment in offspring varies between none in many species of fish to prolonged periods of parental care in birds and mammals (Clutton-Brock 1991). Care of infants by individuals that are not parents occurs in cooperative breeding systems when either siblings, social group members, or polyandrous males help provision and care for young (Moehlman 1986, 1988; Brown 1987; Clutton-Brock 1991). Levels of parental care by males and females vary between species.

Since all mammalian infants require milk for survival, all mammalian mothers care for their infants post-parturition. Milk is energetically expensive to produce and lactating females must increase their intake of energy and, to varying degrees, water (Oftedal 1984, 1985). Increased water and forage requirements force lactating females of some species to change their patterns of habitat use from those of their non-lactating cohorts; the Grevy's zebra *(Equus grevyi)* is one such species (Ginsberg 1988).

The Grevy's zebra is endemic to the semi-arid regions

of northern Kenya, southern Ethiopia and Somalia. Compared to camels and other ruminant ungulates of semi-arid and arid regions, Grevy's zebra are very water dependent (Taylor et al. 1970; Yagil 1985; Wilson 1989). Non-lactating adults need to drink every few days while lactating mares drink daily (Klingel 1967,1974; Ginsberg 1988). Water availability controls where Grevy's zebra can graze within their home range. Lactating females remain within a few kilometers of water while animals in different reproductive stages can graze > 10 km from water (Klingel 1974, Ginsberg 1988).

The social organization of Grevy's zebra is comprised of territorial stallions that maintain territories in areas close to water and/or in areas with good forage, and females and bachelor males that move within, across and outside territories within their home range (Rubenstein 1986, Ginsberg 1988). Females tend to form groups with other females in similar stages of reproduction. No groups are permanent but early lactation females form associations that can last 90 days or more (Ginsberg 1988). These females are generally found within 3 kilometers of water on areas that are defended by territorial stallions (Ginsberg 1988).

Previous studies of this species have questioned how well suited the Grevy's zebra is to its arid environment. Klingel (1977) suggested that the territorial or resource defense social system of Grevy's zebra and African and Asiatic asses (*E. africanus, E. hemionus*) is better suited

to mesic areas whereas the female defense or harem social system of horses, Burchell's and Mountain zebra (*E. caballus, E. burchelli, E. zebra*) is better suited to more xeric conditions. However, Ginsberg (1988) argues that a social system that allows for changes in female movement according to their nutritional and water needs is best suited to the unpredictability of semi-arid environments.

This study focuses on the factors that affect infant survival from parturition to weaning. Three areas are investigated: maternal investment, as measured by milk allocation; maternal ranging patterns and infant survival; and infant behavior and ecology within the mother-infant group. The concluding section of this dissertation summarizes the behavioral and environmental factors which influence infant survival, and addresses how this information can be used for the conservation of this endangered species.

ECOLOGY OF GREVY'S ZEBRA

The social system

Emlen and Oring (1977) developed an ecological model of mating strategies dependent on the abundance and distribution of females, seasonality of breeding, and female-female social relationships. To obtain copulations, males must have access to estrous females. Males can increase their likelihood of paternity by monopolizing

females throughout estrus. Within the genus *Equus* (family Equidae), two mating strategies predominate. Female defense polygamy (harems) occurs when a stallion is able to monopolize a cohesive group of females. Resource defense polygamy occurs when a stallion maintains exclusive mating rights within a defendable territory. Males with better territories, those which best fit the requirements of estrous females, have higher breeding success (Orians 1969; Rubenstein 1986; Ginsberg 1988).

Indigenous and introduced populations of the six species of equids inhabit a variety of desert/steppe and savannah ecosystems in temperate and tropical regions. Harems are typically found in relatively mesic environments. Female membership within groups is static and a dominance hierarchy exists between females (horses - Berger 1986, Duncan et al. 1984; Grant's zebra [*E. burchelli boehmi]* Klingel 1975, Gakathu 1984; and Mountain and Hartmann's zebra [*E. zebra]* Joubert 1972, Penzhorn 1975).

Resource defense polygamy occurs under xeric conditions when one or more resources are limiting. Females form loose associations with other females that can last from several hours to several months. This ever changing social structure occurs in African asses (Moehlman 1974, 1979; Klingel 1977; Woodward 1979), Asiatic asses (Klingel 1975, 1977) and Grevy's zebra (Klingel 1967, 1974, 1975; Rubenstein 1986, 1989; Ginsberg 1988). Associations between

two adult Grevy's zebra lasted from 8 days between non-reproductive females to up to three months between lactating females (Ginsberg 1988). Associations noted between feral African asses are weaker; except for a female and her most recent offspring, two asses were rarely seen together for longer than one week (Moehlman 1974).

The social systems described above are malleable, studies of feral African asses and domestic horses have documented variations in the social systems typically found within these two species. On Assignees Is, a mesic area, female feral African asses formed closed membership groups which are defendable by single stallions (Moehlman 1979, Moehlman pers. comm.; McCort 1980). Feral horses on the Shackleford banks exhibit a variety of social groupings depending on female movement patterns and intra-female social relationships (Rubenstein 1986). Females form long-term female-female associations in areas where forage is evenly distributed and less permanent associations where forage is unevenly distributed. Three types of mating-social systems are found: multi-female harems, male defended territories with groups of females, and (at least temporarily) monogamous male-female associations (Rubenstein 1986).

Reproductive requirements of Grevy's zebra

Because Grevy's zebra inhabit areas with variable