

# Contents

Preface	xi
<b>1</b> History and Natural History	1
1.1 Taxonomy and Phylogeny	3
1.2 Social Organization	4
1.3 Ecology	7
1.4 Conservation Issues	7
1.5 Issues Addressed by the Research and Organization of the Book	11
<b>2</b> The Selous, the Study Population, and General Methods	15
2.1 The Selous Game Reserve	15
2.2 The Study Area and Population	23
2.3 General Methods	25
<b>3</b> Home Ranges and Habitat Selection	36
3.1 Specific Methods	36
3.2 Description of Home Ranges	39
3.3 Exclusive Areas, Overlaps and Territorial Defense	41
3.4 Den Locations and Characteristics	50
3.5 Pack Size and Range Size	51
3.6 Habitat Selection	52
3.7 Effect of Prey Distribution on Habitat Selection and Home Range Properties	55
3.8 Comparison with Other Wild Dog Populations	59
3.9 Summary	65
<b>4</b> Cooperative Hunting and the Evolution of Sociality	67
4.1 Specific Methods	69
4.2 Hunting and Foraging Success	73
4.3 Prey Selection and Hunting Success	74
4.4 Cooperative Hunting Behavior	76
4.5 Characteristics of Kill Sites	84

4.6	Quantitative Effects of Pack Size on Hunting Benefits and Costs	84
4.7	Optimal Hunting Pack Size	88
4.8	Net Rate of Food Intake vs. Efficiency	89
4.9	Effects of Group Size Unrelated to Hunting	95
4.10	Variance in Foraging Success	96
4.11	Other Wild Dog Populations	97
4.12	Communal Hunting and Group Size: Comparisons with Other Species	98
<b>5</b>	<b>Prey Selection</b>	<b>103</b>
5.1	Prey Availability and Encounter Rates	105
5.2	Encounters and Hunts	109
5.3	Hunts and Kills	111
5.4	Combined Effects of Encounter, Hunting, and Killing Probabilities on Prey Selection	112
5.5	Quantitative Models of Prey Selection	114
5.6	Summary	122
<b>6</b>	<b>Ungulate Herd Sizes and the Risk of Predation by Wild Dogs</b>	<b>124</b>
6.1	Probability of Being Encountered	126
6.2	The Probability of Being Hunted upon Encounter	130
6.3	Hunting Success	130
6.4	Kills per Encounter, Dilution of Risk, and Combined Measures of Vulnerability	133
<b>7</b>	<b>Demography—Survival and Reproduction</b>	<b>145</b>
7.1	Survival Rates	145
7.2	Reproduction	159
7.3	Density Dependence	173
7.4	Genetic Effective Population Size	175
7.5	Demographic Effective Population Size	176
<b>8</b>	<b>Dispersal</b>	<b>179</b>
8.1	Defining Dispersal in Social Carnivores	181
8.2	Number and Size of Dispersing Groups	184
8.3	Rates of Dispersal	184
8.4	Size of Dispersing Groups	184

8.5	Linear Dispersal Distance	186
8.6	The Duration and Circumstances of Floating	187
8.7	Comparison with Dispersal in Other Wild Dog Populations	190
8.8	Mortality Risk of Dispersal	191
8.9	Dispersal and Escape from Reproductive Suppression	194
8.10	Dispersal and Escape from Inbreeding	195
8.11	Integrating Forces that Drive Dispersal	200
<b>9</b>	<b>Reproductive Suppression, Social Stress, and the Behavioral and Endocrine Correlates of Rank</b>	<b>201</b>
9.1	Are Dominants More Aggressive?	205
9.2	Do Dominants Mate More Often or More Effectively?	207
9.3	Do Hormonal Differences Accompany Behavioral Differences?	210
9.4	Nonbreeder Lactation	214
9.5	Does Social Stress Mediate Reproductive Suppression of Subordinates?	215
9.6	How Effective Is Reproductive Suppression of Subordinates?	216
9.7	Similarities and Differences between the Sexes in the Correlates of Rank	217
9.8	Interspecific Comparisons	218
9.9	Dominance and Stress	218
9.10	Do the Correlates of Rank Relate to Dispersal and Social Organization?	222
<b>10</b>	<b>Patterns of Relatedness and the Fitness Consequences of Dispersal, Philopatry, and Reproductive Suppression</b>	<b>223</b>
10.1	Age-specific Relatedness of Natal and Immigrant Subordinates to Breeders	226
10.2	Inclusive Fitness of Nondispersers	231
10.3	Inclusive Fitness of Dispersers	238
10.4	Incomplete Reproductive Suppression: Breeding by Subordinates	240

11	Interspecific Competition with Larger Carnivores	245
11.1	Specific Methods	246
11.2	Carnivore Densities and Distributions in Selous	248
11.3	Correlations between Species Densities	253
11.4	Diet Overlap	257
11.5	Direct Competition at Kills	259
11.6	Interactions Away from Kills	263
11.7	Impact of Interspecific Competition	265
11.8	Adaptations to Interspecific Competition	266
12	Infectious Diseases	269
12.1	Canine Distemper Virus	271
12.2	Rabies Virus	274
12.3	Anthrax	277
12.4	Canine Parvovirus	279
12.5	Other Pathogens	281
12.6	Behavior and Epidemiology	284
12.7	Impact of Diseases on Population Dynamics and Density	286
13	Extinction Risk and Conservation	288
13.1	Analysis of Extinction Risk with Leslie Matrix Projections	290
13.2	Stochastic Individual-Based Modeling of Extinction Risk	295
13.3	Sensitivity Analysis and Results	298
13.4	Summary and Recommendations	308
	References	311
	Index	339

## Preface

*The theorist imagines his companions as a naive Romeo imagined his ideal Juliet. The experimenter's lovers sweat, complain, and fart.*

—James Gleick, *Chaos*

In the last fifteen years, African wild dogs have made a lot of progress. After many years of languishing in the shadows of Africa's better-known carnivores, wild dogs have recently been the focus of many studies and conservation efforts scattered across the continent. Much of the recent interest in wild dogs has been spurred by the realization that wild dogs face an uncertain future. In the 1980s, George and Lori Frame conducted a continentwide survey and concluded that only some 5,000 wild dogs survived in sub-Saharan Africa. Worse, the species' range was contracting and some populations were shrinking. For reasons that were not well understood at the time of the Frames's survey, wild dogs always live at low densities, and frequently disappear from protected areas that function perfectly well for the conservation of lions, hyenas, and leopards.

Spurred by the recognition that wild dogs are at risk of extinction, masses of information have been gathered in wild dog studies by Gus Mills, Martyn Gorman, and Anthony Maddock in South Africa; Tico McNutt in Botswana; Josh Ginsberg and Greg Rasmussen in Zimbabwe; and a long series of scientists in Northern Tanzania, including George and Lori Frame, Hugo van Lawick, James Malcolm, Clare Fitzgibbon, John Fanshawe, Todd Fuller, Pieter Kat, Karen Laurenson, Stephen Lelo, and Roger Burrows. Reintroduction efforts in South Africa, Tanzania, and Namibia have met with mixed success, but generally provide hope that the wild dogs' decline can not only be stopped, but reversed.

In addition to answering questions posed by conservation concerns, field studies of wild dogs have made basic contributions to the fields of ecology and animal behavior. In particular, wild dogs have been excellent subjects for studies of cooperation and group living, hunting behavior, social behavior, and interspecific competition.

Against this background, the intention of this book is to present the data from our study of African wild dogs in the Selous Game Reserve, which ran from 1991 to 1997. We compare our results to other studies of wild dogs and to studies of other carnivores and social species. The book is aimed at pro-