



LARGE CARNIVORES

AND THE CONSERVATION OF

BIODIVERSITY

■ EDITED BY
Justina C. Ray
Kent H. Redford
Robert S. Steneck
Joel Berger

About Island Press

Island Press is the only nonprofit organization in the United States whose principal purpose is the publication of books on environmental issues and natural resource management. We provide solutions-oriented information to professionals, public officials, business and community leaders, and concerned citizens who are shaping responses to environmental problems.

In 2005, Island Press celebrates its twenty-first anniversary as the leading provider of timely and practical books that take a multidisciplinary approach to critical environmental concerns. Our growing list of titles reflects our commitment to bringing the best of an expanding body of literature to the environmental community throughout North America and the world.

Support for Island Press is provided by the Agua Fund, Brainerd Foundation, Geraldine R. Dodge Foundation, Doris Duke Charitable Foundation, Educational Foundation of America, The Ford Foundation, The George Gund Foundation, The William and Flora Hewlett Foundation, Henry Luce Foundation, The John D. and Catherine T. MacArthur Foundation, The Andrew W. Mellon Foundation, The Curtis and Edith Munson Foundation, National Environmental Trust, The New-Land Foundation, Oak Foundation, The Overbrook Foundation, The David and Lucile Packard Foundation, The Pew Charitable Trusts, The Rockefeller Foundation, The Winslow Foundation, and other generous donors.

The opinions expressed in this book are those of the author(s) and do not necessarily reflect the views of these foundations.

Large Carnivores and the Conservation of Biodiversity

Large Carnivores and the Conservation of Biodiversity

EDITED BY

*Justina C. Ray, Kent H. Redford,
Robert S. Steneck, and Joel Berger*

 **ISLANDPRESS**

Washington • Covelo • London

Copyright © 2005 Island Press

All rights reserved under International and Pan-American Copyright Conventions. No part of this book may be reproduced in any form or by any means without permission in writing from the publisher: Island Press, 1718 Connecticut Ave., NW, Suite 300, Washington, DC 20009.

ISLAND PRESS is a trademark of The Center for Resource Economics.

Library of Congress Cataloging-in-Publication data.

Large carnivores and the conservation of biodiversity /
edited by Justina C. Ray . . . [et al.].

p. cm.

Includes bibliographical references and index.

ISBN 1-55963-079-5 (cloth : alk. paper) — ISBN 1-55963-080-9
(pbk. : alk. paper)

1. Carnivora—Conservation. 2. Carnivora—Ecology.
3. Predation (Biology) 4. Biological diversity conservation.
I. Ray, Justina C.

QL737.C2C794 2005

591.716—dc22

2004021349

British Cataloguing-in-Publication data available.

Printed on recycled, acid-free paper ♻️

Design by Paul Hotvedt

Manufactured in the United States of America

10 9 8 7 6 5 4 3 2 1

Contents

Acknowledgments xi

CHAPTER 1

Introduction: How to Value Large Carnivorous Animals 1

Kent H. Redford

PART I

Setting the Stage 7

CHAPTER 2

An Ecological Context for the Role of Large Carnivores in
Conserving Biodiversity 9

Robert S. Steneck

"The World Is Green" Revolution 10

Paradigm Gained—Predation as a Structuring Process 11

Top-Down Forces in Food Webs: Keystones to Trophic Cascades 15

Variability of Trophic Cascades 17

Do Marine Systems Have the Strongest Trophic Cascades? 23

Why Big Fierce Animals Are Rare: Top-Down Vulnerability and Chronically
Sliding Baselines 26

Conserving Biodiversity 30

Summary 32

CHAPTER 3

Large Carnivorous Animals as Tools for Conserving Biodiversity: Assumptions
and Uncertainties 34

Justina C. Ray

Large Carnivorous Animals as Conservation Tools 37

Assumptions Underlying the Use of Large Carnivores as Conservation Tools 45

viii Contents

Testing the Assumptions behind Using Large Carnivores as Conservation Tools	48
Conservation Implications: Large Carnivorous Animals in Conservation Practice	53
Summary	55

PART II

The Scientific Context for Understanding the Role of Predation	57
--	----

CHAPTER 4

Carnivory and Trophic Connectivity in Kelp Forests	61
--	----

James A. Estes

The Sea Otter–Kelp Forest Ecosystem	63
Implications for Other Species and Ecosystems	74
Implications for Conservation and Management	78
Summary	80

CHAPTER 5

The Green World Hypothesis Revisited	82
--------------------------------------	----

John Terborgh

Tests of the Plant Self-Defense Hypothesis	84
Predator Exclusion Experiments	88
Nature Reduced to an Artifact	94
Conservation Recommendations	97
Summary	97

CHAPTER 6

Restoring Functionality in Yellowstone with Recovering Carnivores: Gains and Uncertainties	100
---	-----

Joel Berger and Douglas W. Smith

Ecology in Yellowstone National Park with and without Wolves	101
Ecology beyond Yellowstone National Park with and without Wolves	107
Summary	108

CHAPTER 7

Large Marine Carnivores: Trophic Cascades and Top-Down Controls in Coastal Ecosystems Past and Present 110

Robert S. Steneck and Enric Sala

Predation Theory and Evidence of Effects 111

We Eat Large Marine Carnivores: Fisheries-Induced Declines in Predator Abundance 112

Evidence for Past and Present Top-Down Predator Effects Altering Trophic Cascades in Major Benthic Marine Ecosystems 116

Evidence from Other Marine Ecosystems 132

General Consequences of the Loss of Large Carnivores, and Implications for Conservation 134

Summary 136

CHAPTER 8

Forest Ecosystems without Carnivores: When Ungulates Rule the World 138

William J. McShea

Extent of the Problem of High-Density Ungulate Populations 138

Ungulate Effects on Biodiversity 142

Is There Evidence That Reducing Ungulate Density Restores Biodiversity? 147

Hunters versus Large Carnivores 148

Conservation Recommendations 150

Summary 152

CHAPTER 9

King of the Beasts? Evidence for Guild Redundancy among Large Mammalian Carnivores 154

Rosie Woodroffe and Joshua R. Ginsberg

Large Carnivore Assemblages and the Forces That Structure Them 159

When Guilds Collapse: Rules for the Disassembly of Large Carnivore Assemblages 160

Guild Redundancy and Compensation 162

x Contents

Conserving Complete Large Carnivore Guilds in Fragmented Landscapes: Some Complex and Surprising Predictions	169
Conclusions and Conservation Recommendations	172
Summary	174

PART III

From Largely Intact to Human-Dominated Systems: Insight on the Role of Predation Derived from Long-Term Studies	177
--	-----

CHAPTER 10

Tigers and Wolves in the Russian Far East: Competitive Exclusion, Functional Redundancy, and Conservation Implications	179
---	-----

*Dale G. Miquelle, Philip A. Stephens, Evgeny N. Smirnov, John M. Goodrich, Olga J.
Zaumyslova, and Alexander E. Myslenkov*

Study Areas	180
Data Analysis and Modeling Methods	182
Research Findings	186
Competitive Exclusion and Functional Redundancy in Tigers and Wolves	200
Conservation Implications	203
Summary	205

CHAPTER 11

Large Carnivores and Biodiversity in African Savanna Ecosystems	208
---	-----

M. G. L. Mills

Study Areas	209
Predator–Prey Relationships in Various Systems	212
Intraguild Relationships	223
Biodiversity Implications of Large Carnivore Ecology	223
Conserving Carnivores and Carnivory in Ecosystems	225
Ecosystems without Carnivores and Other Conservation Implications	227
Summary	228

CHAPTER 12**Large Carnivores and Ungulates in European Temperate Forest Ecosystems:
Bottom-Up and Top-Down Control 230***Bogumiła Jędrzejewska and Włodzimierz Jędrzejewski*

Białowieża Primeval Forest: Study Area and Methods 231

Wolf and Lynx Predation on Ungulates 233

Long-Term Data on Large Carnivores and Ungulates 236

Top-Down and Bottom-Up Forces in Diverse Guilds of Predators and Prey 240

Trophic Cascades: Indirect Effects of Large Carnivores on Forest Ecosystems 242

Conservation Implications 244

Summary 245

CHAPTER 13**Recovery of Carnivores, Trophic Cascades, and Diversity in Coral Reef
Marine Parks 247***Tim R. McClanahan*

Statement of the Problem 249

Study Sites and History of the Coral Reef Parks 249

Field Sampling and Data Analysis 251

Research Findings 254

Discussion 261

Conservation Recommendations and Concluding Thoughts 264

Summary 266

CHAPTER 14**Human-Induced Changes in the Effect of Top Carnivores on Biodiversity in
the Patagonian Steppe 268***Andrés J. Novaro and R. Susan Walker*

Native Carnivore and Prey Communities of the Patagonian Steppe 269

Human Impact on Patagonian Wildlife 271

Effects on Wildlife of Reduction of Sheep and Hunting 273

Possible Top-Down Control of Native Herbivores by Pumas and Culpeos 276

Predation as a Potential Threat to Wildlife Conservation in Patagonia 282

xii Contents

Conservation Recommendations 284
Concluding Thoughts: How Unique Is the Patagonian Example? 287
Summary 287

PART IV

**Achieving Conservation and Management Goals through Focus on Large
Carnivorous Animals 289**

CHAPTER 15

**Large Carnivores, Herbivores, and Omnivores in South Florida:
An Evolutionary Approach to Conserving Landscapes and
Biodiversity 293**

David S. Maehr, Michael A. Orlando, and John J. Cox

Study Area 295
The Bear and the Weevil 297
Felid Predators and Deer 301
Wolves and Big Cypress Deer 306
The Challenge to Managers 309
Summary 313

CHAPTER 16

**Hunting by Carnivores and Humans: Does Functional Redundancy Occur and
Does It Matter? 315**

Joel Berger

Limitations of Approach 316
Current Overlap between Hunting Humans and Carnivores 317
Predictions: Concordance in Effects of Human and Carnivore Hunting 319
Conservation Recommendations: Functionality in Systems with Carnivores
and Humans 337
Summary 340

CHAPTER 17**Detecting Top-Down versus Bottom-Up Regulation of Ungulates by Large Carnivores: Implications for Conservation of Biodiversity 342***R. Terry Bowyer, David K. Person, and Becky M. Pierce*

Conceptual Models of Predator–Prey Dynamics 344

Failure to Consider Effects of K 346

Prey to Predator Ratios 349

Kill Rates 351

A Prey-Based Approach for Understanding Top-Down and Bottom-Up Processes 354

Future Directions for Predator–Prey Modeling 358

Linking Predator–Prey Dynamics to Ecosystem Processes and Biodiversity 359

Summary 360

CHAPTER 18**Top Carnivores and Biodiversity Conservation in the Boreal Forest 362***Stan Boutin*

The Boreal Forest Context 364

How Do Carnivores Affect the Boreal Forest? 366

Top Carnivores as Umbrellas for Biodiversity 377

A Biodiversity Conservation Approach Focused on Maintaining the Range of Natural Variability 378

Summary 379

CHAPTER 19**The Linkage between Conservation Strategies for Large Carnivores and Biodiversity: The View from the “Half-Full” Forests of Europe 381***John D. C. Linnell, Christoph Promberger, Luigi Boitani, Jon E. Swenson, Urs Breitenmoser, and Reidar Andersen*

The Nature of Biodiversity 382

Europe: A Continent Shaped by Humans 382

European Large Carnivore Populations 386

Goals for Large Carnivore Conservation in Europe 389

How Does Conserving Carnivores Conserve Biodiversity in Europe? 394

xiv Contents

Is Europe Unique? 396
Conservation Recommendations 397
Summary 398

CHAPTER 20

**Conclusion: Is Large Carnivore Conservation Equivalent to Biodiversity
Conservation and How Can We Achieve Both? 400**

Justina C. Ray, Kent H. Redford, Joel Berger, and Robert Steneck

Framing the Question 401
The Link between Large Carnivorous Animals and Biodiversity 401
Where There Is Strong Evidence for Biodiversity Impacts through Predation by Large
Carnivorous Animals 403
Where the Evidence Is Less Compelling or Absent 405
Unknowns and Unknowable 409
Is Carnivore Conservation Compatible with Biodiversity Conservation? 411
Large Carnivores as Conservation Tools 415
Conservation Recommendations: Achieving Carnivore and
Biodiversity Conservation 419
Concluding Thoughts 425
Summary 426

References 429
List of Contributors 509
Index 512

Acknowledgments

We are grateful to the attendants of the workshop held at the White Oak Plantation in May 2003, of which this volume is a direct result. They generously contributed their time and thoughts to addressing the complicated set of questions we have posed here, and then spent considerable energy formulating these beautifully written essays in a relatively rapid timeframe. Thanks also to nonattending coauthors who enthusiastically shared their expertise, often with very short notice, to fill critical gaps in our coverage. It was our sincere pleasure and honor to work with such high-caliber scientists.

All chapters of this volume benefited enormously from rigorous reviews provided by the following individuals, who generously donated their time and creative energy to improve clarity and content of each contribution: Liz Bennett, Richard Bodmer, Luigi Boitani, Stan Boutin, Terry Bowyer, Rodrigo Bustamante, Carlos Carroll, Emmett Duffy, Sarah Durant, Jim Estes, Graham Forbes, Todd Fuller, Josh Ginsberg, Jodi Hilty, Luke Hunter, John Linnell, David Maehr, Tim McClanahan, Bill McShea, Brian Miller, Reed Noss, François Messier, Andrés Navarro, Tim O'Brien, John Robinson, Mel Sunquist, Rick Sweitzer, and Adrian Treves. To all we are grateful.

Barbara Dean at Island Press was a bottomless source of enthusiasm from the moment she heard the first seeds of our proposal. She and Barbara Youngblood responded to each and every query, guiding us with steady hands through the small details and the complexities alike. The preparation of this volume in the relatively short timeframe from conception to printing would simply not have been possible without the cheerful and able assistance of Joanna Zigouris, whose careful attention to detail and understanding of the process helped at every turn of the way.

The workshop was made possible through the generous support of the White Oak Conservation Center of Gilman International Conservation. In particular we thank John Lukas. We gratefully acknowledge the Wildlife Conservation Society for its support through the development of the volume. Finally, we extend our deep appreciation for the patience and encouragement of our families.