

# Hormones and Reproduction in Fishes, Amphibians, and Reptiles

# Hormones and Reproduction in Fishes, Amphibians, and Reptiles

Edited by

David O. Norris  
and

Richard E. Jones

University of Colorado  
Boulder, Colorado

Plenum Press • New York and London

---

Library of Congress Cataloging in Publication Data

Hormones and reproduction in fishes, amphibians, and reptiles.

Includes bibliographies and index.

1. Fishes—Reproduction—Endocrine aspects. 2. Amphibians—Reproduction—Endocrine aspects. 3. Reptiles—Reproduction—Endocrine aspects—Congresses. 4. Endocrinology, Comparative. I. Norris, David O. II. Jones, Richard E. (Richard Evan), 1940-

QL639.2.H67 1987

597

87-6944

ISBN-13: 978-1-4612-9042-1

e-ISBN-13: 978-1-4613-1869-9

DOI: 10.1007/978-1-4613-1869-9

---

© 1987 Plenum Press, New York  
Softcover reprint of the hardcover 1st edition 1987  
A Division of Plenum Publishing Corporation  
233 Spring Street, New York, N.Y. 10013

All rights reserved

No part of this book may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, microfilming, recording, or otherwise, without written permission from the Publisher

We dedicate this volume to our teachers and mentors, Professor Howard A. Bern and Professor Aubrey Gorbman, and to all those to whom we have taught the excitement of comparative endocrinology that Professors Bern and Gorbman instilled in us.

## PREFACE

Comparative endocrinology is one of the most rapidly developing subdisciplines within the field of endocrinology, and it is having a significant impact on research at the molecular, cellular, organismal and environmental levels. Much of the current ferment in endocrinology is in reproductive endocrinology. The purpose of this volume on hormones and reproduction in fishes, amphibians and reptiles is to summarize our present understandings and to identify important research problems to be addressed in the area of comparative reproductive endocrinology. It was inspired by the gathering at Copper Mountain, Colorado, of eminent endocrine scientists from around the world on the occasion of the Tenth International Symposium on Comparative Endocrinology in July, 1985. While preparing for that meeting, we decided that a special volume on reproductive endocrinology was needed to summarize what is known and to stimulate research in particular directions.

Why do we emphasize fishes, amphibians and reptiles? First, knowledge about the reproductive endocrinology of these ectothermic vertebrates can provide a clearer picture of the evolution of reproductive hormones and their effects on target organs. This comparative approach can lead to new theories about the evolution of reproductive control mechanisms.

Second, studies concerning the reproductive endocrinology of "lower" vertebrates can result in development of "model systems" for application to studies of birds and mammals. Indeed, information about the patterns of reproductive control in ectothermic vertebrates can tell us which are evolutionarily stable and which are labile. This historical perspective then can lead to predictions about reproductive control mechanisms in birds and mammals which have separate evolutionary origins from ectothermic reptiles. Even without enough information to form an evolutionary history, specific discoveries from, for example, a frog or lizard species can be tested in mammals. Contributions from such approaches are being made at all levels. Professor Howard A. Bern (1984) summarized this for us:

. . . in recent years, has come the recognition that comparative endocrinology can break new ground: can discover new phenomena

and offer new concepts, which are then applicable to an understanding of endocrine physiology generally--in mammals and in humans.

Third, some ectothermic vertebrates are important food sources. This is especially true for fishes but also for some amphibians and reptiles. And, with the present state of human population growth, these ectothermic vertebrates will become more important economically in the future. In this regard, reproductive endocrinology has, and will continue to have, important benefits related to the propagation of certain food species (e.g., salmon, bullfrogs, green sea turtles).

Fourth, several ectothermic vertebrate species are endangered and could become extinct. Besides protection and habitat management, it will become necessary to house breeding stocks of endangered species as captive populations, and the utilization of hormonal manipulations may be a valuable tool for propagating these species for eventual release into nature. For example, synthetic gonadotropin-releasing hormone is now being used to induce ovulation in captive, endangered anuran amphibians.

Lastly, the reproductive biology of a species plays a vital role in its natural history and life cycle. Therefore, knowledge about the reproductive endocrinology of any species can fill an important gap in our understanding of its particular adaptations. Such knowledge will be essential for future management of natural habitats and for perpetuation of natural populations.

The topics chosen for this work include development and differentiation, gonadal cycles, oocyte maturation, vitellogenesis, ovulation, corpus luteum function, male gonaducts and sex accessory glands, steroid receptors and binding proteins, behavior, evolution of viviparity, aging of the neuroendocrine-reproductive axis, and the roles of gonadotropin-releasing hormones, gonadotropins, prolactin, thyroid hormones, steroid hormones, stress hormones, the pineal complex and environmental factors. The contributors are some of the current leaders in comparative endocrinology of ectothermic vertebrates, and they represent six countries evenly distributed among the three continents: Asia, Europe and North America.

It is the editors' hope and intention that this volume will not only serve as an introduction to specific topics in comparative reproductive endocrinology but also will stimulate new research in the field. We have attempted to coordinate the chapters contributed by the various authors through the use of cross-references. Furthermore, we have adhered as much as possible to a uniform terminology as well as a standard format for each chapter, beginning with mammalian (and where pertinent, avian) knowledge followed by discussions of fishes, amphibians and reptiles.

We wish to thank all of the contributors for their hard work, tolerance and patience. Frank Moore kindly supplied us with the cover photograph. Finally, special thanks go to Ann Underwood for typing the camera-ready copy and to Plenum Publishing Corporation for their support.

Boulder, Colorado

David O. Norris  
Richard E. Jones

CONTENTS

CHAPTER 1

HORMONES AND SEXUAL DIFFERENTIATION

Elizabeth Adkins-Regan

I.	Introduction. . . . .	1
A.	Sex Determination . . . . .	1
II.	Theoretical and Conceptual Context . . . . .	4
A.	Organization vs. Activation: Critical Periods. . . . .	4
B.	Adult Sexual Dimorphism . . . . .	5
C.	The Nature of the Inducer(s) . . . . .	5
III.	Differentiation of the Gonads . . . . .	6
A.	Fishes . . . . .	6
B.	Amphibians . . . . .	8
C.	Reptiles . . . . .	10
IV.	Differentiation of Other Reproductive Structures. . . . .	10
A.	Fishes. . . . .	10
B.	Amphibians. . . . .	11
C.	Reptiles. . . . .	11
V.	Differentiation of Behavior and the Nervous System. . . . .	12
A.	Fishes. . . . .	12
B.	Amphibians. . . . .	14
C.	Reptiles . . . . .	15
VI.	Temperature and Sexual Differentiation. . . . .	16
VII.	Environmental Hermaphroditism and Social Influences on Sexual Differentiation . . . . .	18
A.	Fishes. . . . .	18
VIII.	Summary and Conclusions . . . . .	20
A.	The Nature of the Inducer(s). . . . .	20
B.	How Useful is the Organizational Theory? . . . . .	21
C.	Relationship Between Sex Determination and Differentiation. . . . .	21
D.	Differentiation and Epigenesis. . . . .	22
IX.	Acknowledgments . . . . .	22
X.	References. . . . .	23



CHAPTER 2

GONADOTROPIN-RELEASING HORMONES IN FISHES

Nancy Sherwood

- I. The primary Structure of Known GnRH Family Members . . . . . 31
  - A. Overview of Mammals and Birds . . . . . 31
  - B. Fishes. . . . . 33
  - C. Amphibians and Reptiles . . . . . 34
  
- II. Characterization of New GnRH Molecules in Fishes. . . . . 34
  - A. Agnatha . . . . . 34
  - B. Chondrichthyes. . . . . 36
  - C. Osteichthyes. . . . . 36
    - 1. Nonteleosts . . . . . 36
    - 2. Teleosts. . . . . 36
  
- III. Anatomical Location of GnRH in Fish Brain . . . . . 38
  - A. Agnatha . . . . . 38
  - B. Chondrichthyes. . . . . 38
  - C. Osteichthyes. . . . . 39
  
- IV. Reproductive Responses to GnRH. . . . . 40
  - A. Agnatha . . . . . 41
    - 1. Gonadotropins (Gns) . . . . . 41
    - 2. Steroids. . . . . 41
    - 3. Ovulation . . . . . 41
  - B. Chondrichthyes. . . . . 41
    - 1. Gonadotropins . . . . . 41
    - 2. Steroids. . . . . 42
    - 3. Ovulation . . . . . 42
  - C. Osteichthyes: Nonteleosts. . . . . 42
    - 1. Gonadotropins . . . . . 42
    - 2. Steroids. . . . . 42
    - 3. Ovulation . . . . . 42
  - D. Osteichthyes: Teleosts . . . . . 42
    - 1. Gonadotropins . . . . . 42
    - 2. Steroids. . . . . 45
    - 3. Ovulation and Spawning. . . . . 46
  
- V. Summary and Future Research Directions . . . . . 47
  - A. Evolution of the GnRH Family . . . . . 47
  - B. The Primary Structure of GnRH in Other Fishes. . . . . 48
  - C. Multiple Forms of GnRH in Single Species of Fish . . . . . 50
  - D. Other Roles for GnRH in Fishes . . . . . 51
  - E. Inhibitory Effects of GnRH . . . . . 52
  - F. A Possible GnRIF . . . . . 52
  - G. The Nature of Fish GnRH Receptors. . . . . 52
  - H. The Fish GnRH Precursor(s) . . . . . 53
  
- VI. Acknowledgments. . . . . 53
  
- VII. References . . . . . 53

CHAPTER 3

ROLE OF GONADOTROPIN-RELEASING HORMONE IN REGULATION OF GONADOTROPIN SECRETION FROM AMPHIBIAN AND REPTILIAN PITUITARIES

Paul Licht and David Porter

I.	Identification and Chemical Characterization of GnRH. . . . .	62
A.	Amphibians. . . . .	62
1.	Changes in Endogenous GnRH. . . . .	63
2.	Biochemistry of GnRH. . . . .	64
B.	Reptiles. . . . .	65
1.	Biochemical Characterization. . . . .	66
II.	Regulation of Pituitary Gonadotropin Release: <u>In vivo</u> studies. . . . .	67
A.	Amphibians. . . . .	67
B.	Reptiles. . . . .	72
III.	<u>In vitro</u> Characterization of Pituitary Responsiveness to GnRH . . . . .	73
A.	Amphibians. . . . .	73
B.	Reptiles. . . . .	74
IV.	Mechanism of Action of GnRH . . . . .	77
V.	Future Research Directions. . . . .	78
VI.	Acknowledgment. . . . .	80
VII.	References. . . . .	80

CHAPTER 4

PROLACTIN AND REPRODUCTION

Valdo Mazzi and Camillo Vellano

I.	Prolactin Receptors . . . . .	87
A.	Overview of Mammals . . . . .	87
B.	Fishes. . . . .	88
C.	Amphibians. . . . .	89
D.	Reptiles. . . . .	90
II.	Effects of Prolactin on Gonads, Sexual Accessories and on Secondary Sexual Characters . . . . .	90
A.	Overview of Mammals . . . . .	90
B.	Fishes. . . . .	92
C.	Amphibians. . . . .	92
D.	Reptiles. . . . .	94
III.	Prolactin and Adaptations to the Reproductive Environment . . . . .	94
A.	Overview of Mammals . . . . .	94

B. Fishes. . . . .	95
C. Amphibians. . . . .	98
D. Reptiles. . . . .	101
IV. Prolactin and Reproductive Behavior . . . . .	102
A. Overview of Mammals . . . . .	102
B. Fishes. . . . .	102
1. Migration . . . . .	102
2. Sexual Behavior . . . . .	103
3. Parental Behavior . . . . .	103
C. Amphibians. . . . .	104
1. Water Drive . . . . .	104
2. Sexual Behavior . . . . .	104
3. Parental Care . . . . .	105
D. Reptiles. . . . .	105
V. Summary and Future Research Directions. . . . .	105
VI. References. . . . .	106

CHAPTER 5

REGULATION OF OVARIAN STEROIDOGENESIS

G. Chieffi and R. Pierantoni

I. Introduction. . . . .	117
II. Overview of Mammals . . . . .	117
III. Ovarian Morphology. . . . .	119
A. Cyclostomes . . . . .	120
B. Elasmobranchs. . . . .	120
C. Teleosts. . . . .	121
D. Amphibians. . . . .	121
E. Reptiles. . . . .	122
IV. Sites of Steroidogenesis. . . . .	122
A. Cyclostomes. . . . .	123
B. Elasmobranchs. . . . .	123
C. Teleosts. . . . .	123
D. Amphibians. . . . .	125
E. Reptiles. . . . .	126
V. Steroid Identification and Biosynthesis . . . . .	126
A. Cyclostomes . . . . .	126
B. Elasmobranchs . . . . .	127
C. Teleosts. . . . .	127
D. Amphibians. . . . .	128
E. Reptiles. . . . .	128
VI. Seasonal Profiles . . . . .	128
A. Cyclostomes . . . . .	129
B. Elasmobranchs . . . . .	129
C. Teleosts. . . . .	129
D. Amphibians. . . . .	130
E. Reptiles. . . . .	130

VII.	Gonadotropic Control of Folliculogenesis and Steroidogenesis . .	131
	A. Cyclostomes . . . . .	131
	B. Elasmobranchs . . . . .	131
	C. Teleosts . . . . .	132
	D. Amphibians . . . . .	133
	E. Reptiles . . . . .	134
VIII.	Local Control of Steroidogenesis . . . . .	135
IX.	Summary and Future Research Directions . . . . .	136
X.	References . . . . .	137

CHAPTER 6

ENDOCRINOLOGY OF VITELLOGENESIS

Shuk-mei Ho

I.	Introduction . . . . .	145
II.	Vitellogenin and Vitellogenin Genes. . . . .	146
	A. Fishes. . . . .	146
	B. Amphibians. . . . .	147
	C. Reptiles. . . . .	148
III.	Estrogen Stimulation of Vitellogenin Synthesis and Secretion . .	148
	A. Fishes. . . . .	148
	B. Amphibians. . . . .	149
	C. Reptiles. . . . .	151
IV.	Estrogen Specificity in the Induction of Vitellogenin Synthesis . . . . .	152
	A. Fishes. . . . .	152
	B. Amphibians. . . . .	152
	C. Reptiles. . . . .	153
V.	Influence of Non-estrogenic Steroids on Vitellogenesis. . . . .	153
	A. Fishes. . . . .	153
	B. Amphibians. . . . .	153
	C. Reptiles. . . . .	154
VI.	Influence of Non-steroidal Hormones on Vitellogenesis. . . . .	154
	A. Fishes. . . . .	154
	B. Amphibians. . . . .	154
	C. Reptiles. . . . .	155
VII.	Other Non-hormonal Factors Regulating Vitellogenesis . . . . .	155
	A. Fishes. . . . .	155
	B. Amphibians. . . . .	156
	C. Reptiles. . . . .	156
VIII.	Endocrine Control of Vitellogenin Uptake by Oocytes . . . . .	157
	A. Fishes. . . . .	157
	B. Amphibians. . . . .	158
	C. Reptiles. . . . .	158

IX. Summary of Future Research Directions . . . . .	158
X. References . . . . .	159

CHAPTER 7

ENDOCRINE CONTROL OF OOCYTE MATURATION

Yoshitaka Nagahama

I. Introduction . . . . .	171
II. Primary Hormones Involved in Triggering Oocyte Maturation . . .	173
A. Overview of Mammals . . . . .	173
B. Fishes. . . . .	173
C. Amphibians. . . . .	174
D. Reptiles. . . . .	174
III. Maturation-inducing Substances . . . . .	175
A. Overview of Mammals . . . . .	175
B. Fishes. . . . .	176
C. Amphibians. . . . .	181
D. Reptiles. . . . .	185
IV. Maturation-promoting Factor . . . . .	185
A. Amphibians. . . . .	185
B. Others. . . . .	187
V. Maturation-inhibiting Substances . . . . .	188
A. Overview of Mammals . . . . .	188
B. Fishes. . . . .	189
C. Amphibians. . . . .	190
VI. Summary and Future Research Directions . . . . .	191
VII. Acknowledgments . . . . .	192
VIII. References . . . . .	193

CHAPTER 8

OVULATION: INSIGHTS ABOUT THE MECHANISMS BASED ON A COMPARATIVE APPROACH

Richard E. Jones

I. Introduction . . . . .	203
II. General Description of the Process of Ovulation . . . . .	204
A. Mammals and Birds . . . . .	204
B. Fishes . . . . .	206

C. Amphibians . . . . .	206
D. Reptiles . . . . .	206
III. Cellular Changes in the Follicular Wall Preceding its Rupture. . . . .	207
A. Mammals and Birds . . . . .	207
B. Fishes, Amphibians and Reptiles . . . . .	208
IV. Gonadotropins, Steroid Hormones and Ovulation . . . . .	209
A. Mammals and Birds . . . . .	209
B. Fishes . . . . .	209
C. Amphibians . . . . .	210
D. Reptiles . . . . .	210
V. Prostaglandins and Ovulation . . . . .	210
A. Mammals and Birds . . . . .	210
B. Fishes . . . . .	211
C. Amphibians and Reptiles . . . . .	212
VI. Enzymes and Ovulation . . . . .	212
A. Mammals and Birds . . . . .	212
B. Fishes . . . . .	214
C. Amphibians . . . . .	214
D. Reptiles . . . . .	215
VII. Follicular Contraction and Ovulation . . . . .	215
A. Evidence for a Role of Follicular Contraction in Ovulation . . . . .	215
1. Mammals and Birds . . . . .	215
2. Fishes . . . . .	217
3. Amphibians . . . . .	218
4. Reptiles . . . . .	218
B. Adrenergic and Cholinergic Effects on Follicular Contraction . . . . .	219
1. Mammals and Birds . . . . .	219
2. Teleostean Fishes . . . . .	220
3. Amphibians and Reptiles . . . . .	220
C. Prostaglandins and Follicular Contraction . . . . .	220
D. Oxytocic Hormones and Follicular Contraction . . . . .	221
E. Follicular Wall Tension and Follicular Contraction . . . . .	221
VIII. Summary and Future Research Directions . . . . .	222
IX. Acknowledgments . . . . .	228
X. References . . . . .	228

CHAPTER 9

FUNCTIONAL MORPHOLOGY AND REGULATION OF THE CORPUS LUTEUM

Francoise Xavier

I. Introduction . . . . .	241
II. Formation and Morphology of the Corpus Luteum. . . . .	242
A. Overview of Mammals. . . . .	242

B. Fishes . . . . .	243
C. Amphibians . . . . .	244
D. Reptiles . . . . .	246
III. Hormone Production by the Corpus Luteum. . . . .	248
A. Overview of Mammals. . . . .	248
B. Fishes . . . . .	249
C. Amphibians . . . . .	251
D. Reptiles . . . . .	252
IV. Regulation of Corpus Luteum Activity (Luteotropic Factors) . . .	258
A. Overview of Mammals. . . . .	258
B. Fishes . . . . .	260
C. Amphibians . . . . .	261
D. Reptiles . . . . .	261
V. Regression of the Corpus Luteum (Luteolytic Factors) . . . . .	264
A. Overview of Mammals. . . . .	264
B. Fishes . . . . .	266
C. Amphibians . . . . .	266
D. Reptiles . . . . .	266
VI. Summary and Future Research Directions . . . . .	268
VII. Acknowledgments . . . . .	270
VIII. References . . . . .	271

## CHAPTER 10

### TESTICULAR FUNCTION

Brian Lofts

I. Introduction . . . . .	283
II. Testicular Structure . . . . .	285
A. Fishes . . . . .	285
B. Amphibians . . . . .	288
C. Reptiles . . . . .	288
III. The Spermatogenetic Cycle . . . . .	289
A. Cystic and Non-cystic Spermatogenesis . . . . .	289
B. Spermatogenetic Cyclicity . . . . .	293
1. Fishes . . . . .	293
2. Amphibians . . . . .	294
3. Reptiles . . . . .	295
IV. Steroid Cycles . . . . .	296
A. Steroidogenesis . . . . .	296
1. Fishes . . . . .	296
2. Amphibians . . . . .	297
3. Reptiles . . . . .	298
B. Interstitial Leydig Cells . . . . .	298
1. Fishes . . . . .	298

2. Amphibians . . . . .	299
3. Reptiles . . . . .	300
C. Lobule Boundary Cells . . . . .	301
1. Teleostean Fishes . . . . .	301
2. Amphibians . . . . .	302
D. Sertoli Cells . . . . .	302
1. Fishes . . . . .	302
2. Amphibians . . . . .	304
3. Reptiles . . . . .	305
V. Pituitary-Testis Interrelationships. . . . .	307
A. Fishes . . . . .	307
B. Amphibians . . . . .	310
C. Reptiles . . . . .	311
VI. References . . . . .	314

CHAPTER 11

REGULATION OF MALE GONADUCTS AND SEX ACCESSORY STRUCTURES

David O. Norris

I. Introduction . . . . .	327
II. Wolffian Ducts, Mesonephric Kidneys and Their Derivatives . . . . .	327
A. Fishes . . . . .	329
B. Amphibians . . . . .	330
C. Reptiles . . . . .	333
III. Mullerian Duct Development in Males . . . . .	333
A. Fishes . . . . .	334
B. Amphibians . . . . .	334
C. Reptiles . . . . .	334
IV. Derivatives of the Urogenital Sinus . . . . .	335
A. Fishes . . . . .	335
B. Amphibians . . . . .	335
C. Reptiles . . . . .	336
D. Birds . . . . .	337
V. Intromittant Organs . . . . .	338
A. Fishes . . . . .	338
B. Amphibians . . . . .	339
C. Reptiles . . . . .	339
D. Birds. . . . .	340
VI. Secondary Sexual Characters. . . . .	340
A. Fishes . . . . .	340
B. Amphibians . . . . .	341
C. Reptiles . . . . .	342
VII. The "Paradoxical" Action of Androgens. . . . .	342
VIII. Effects of Arginine Vasotocin on Genital Ducts . . . . .	343



IX.	Summary and Future Research Directions . . . . .	343
	A. Wolffian Duct, Mesonephric Kidneys and Their Derivatives . .	347
	B. Mullerian duct Development in Males . . . . .	347
	C. Derivatives of the Urogenital Sinus . . . . .	347
	D. Secondary Sexual Characters . . . . .	347
	E. The "Paradoxical" Action of Androgens . . . . .	348
X.	Acknowledgments. . . . .	348
XI.	References . . . . .	348

CHAPTER 12

SEX STEROID RECEPTORS AND NON-RECEPTOR BINDING PROTEINS

Ian P. Callard and Gloria V. Callard

I.	Mechanisms of Steroid Hormone Action: An Overview . . . . .	355
	A. Genomic Mechanisms . . . . .	355
	B. Nongenomic Mechanisms. . . . .	357
II.	Receptors. . . . .	358
	A. General Characteristics . . . . .	358
	B. Phylogenetic Distribution . . . . .	359
	C. Major Classes of Steroid Receptors . . . . .	360
	1. Androgen Receptors . . . . .	360
	2. Estrogen Receptors . . . . .	361
	3. Progesterone Receptors . . . . .	361
	D. Receptors in Different Physiological States and Their Regulation . . . . .	366
	1. The Liver and Vitellogenesis . . . . .	366
	2. Gonadal Functions. . . . .	367
	3. Female Reproductive Tract. . . . .	368
	4. Neuroendocrine Tissues . . . . .	369
	5. Other Tissues. . . . .	369
III.	Non-receptor Steroid-Binding Proteins (SBPs) . . . . .	369
	A. General Characteristics. . . . .	369
	B. Phylogenetic and Tissue Distribution . . . . .	370
	C. Functions. . . . .	374
	D. Natural Changes and Regulation of SBPs . . . . .	376
IV.	Summary and Future Directions. . . . .	377
V.	Acknowledgments. . . . .	377
VI.	References . . . . .	378

CHAPTER 13

SEASONAL REPRODUCTION; PATTERNS AND CONTROL

J. M. Whittier and David Crews

I.	Adaptiveness of Seasonality. . . . .	385
A.	Costs of Reproduction. . . . .	387
1.	Fishes . . . . .	387
2.	Amphibians . . . . .	387
3.	Reptiles . . . . .	387
B.	Relation of Reproductive Cycles to other Seasonal Cycles . . . . .	387
II.	Patterns of Reproduction . . . . .	388
A.	Timing of Reproduction . . . . .	388
1.	Fishes . . . . .	388
2.	Amphibians . . . . .	389
3.	Reptiles . . . . .	390
B.	Synchrony and Regularity of Reproduction . . . . .	391
1.	Fishes . . . . .	393
2.	Amphibians . . . . .	393
3.	Reptiles . . . . .	393
III.	Control of Seasonal Reproduction . . . . .	394
A.	Pre-programmed (Closed) vs. Labile (Open) Control. . . . .	394
B.	Endogenous Cycles. . . . .	395
1.	Fishes . . . . .	395
2.	Amphibians . . . . .	395
3.	Reptiles . . . . .	396
C.	Environmental Control. . . . .	396
1.	Fishes . . . . .	396
2.	Amphibians . . . . .	397
3.	Reptiles . . . . .	397
IV.	Neuroendocrine Control of Reproduction . . . . .	398
A.	Mechanisms of Endogenous Control . . . . .	399
B.	Mechanisms of Environmental Control . . . . .	399
1.	Fishes . . . . .	399
2.	Amphibians . . . . .	400
3.	Reptiles . . . . .	401
V.	Summary and Directions for Future Research . . . . .	402
VI.	Acknowledgments. . . . .	404
VII.	References . . . . .	404

CHAPTER 14

THYROID HORMONES AND REPRODUCTION

John F. Leatherland

I.	Introduction . . . . .	411
	A. Control of Thyroid Function . . . . .	411
	B. Interpretations of Observations. . . . .	413
	C. Thyroid Function and Reproduction in Mammals . . . . .	415
II.	Thyroid Hormones and Gonadal Functions . . . . .	417
	A. Fishes . . . . .	417
	B. Amphibians . . . . .	418
	C. Reptiles . . . . .	418
III.	Seasonal Changes in Thyroid Activity . . . . .	419
	A. Fishes . . . . .	419
	B. Amphibians . . . . .	420
	C. Reptiles . . . . .	421
IV.	Thyroid Hormones and Vitellogenesis . . . . .	421
	A. Fishes . . . . .	421
	B. Amphibians . . . . .	422
	C. Reptiles . . . . .	422
V.	Gonadotropins, Gonadal Steroids and Thyroid Economy. . . . .	422
	A. Fishes . . . . .	422
	B. Amphibians . . . . .	423
	C. Reptiles . . . . .	424
VI.	Summary and Future Research Directions . . . . .	424
VII.	Acknowledgment . . . . .	425
VIII.	References . . . . .	425

CHAPTER 15

PINEAL INVOLVEMENT IN SEASONALITY OF REPRODUCTION

William A. Gern, Jeanne M. Nervina, and Shelley S. Greenhouse

I.	Introduction . . . . .	433
II.	Pineal and Reproduction. . . . .	433
	A. Mammalian Overview . . . . .	433
	B. Agnathans. . . . .	435
	C. Teleosts . . . . .	440
	D. Amphibians . . . . .	443
	E. Reptiles . . . . .	449
	1. Males. . . . .	449
	2. Females . . . . .	455
III.	Summary and Directions for Future Research . . . . .	456

IV. Acknowledgments . . . . .	457
V. References . . . . .	457

CHAPTER 16

STRESS AND REPRODUCTION: RECIPROCAL RELATIONSHIPS

Neil Greenberg and John Wingfield

I. Introduction . . . . .	461
A. Background . . . . .	461
B. Definitions . . . . .	462
C. Stress Hormones . . . . .	462
II. Stress Effects on Reproductive Physiology and Behavior . . . . .	465
A. Overview of Mammals . . . . .	465
1. Effects of Stress upon Social and Reproductive Activity . . . . .	465
2. Stress Axis Effects on Gonadal Function . . . . .	468
B. Fishes . . . . .	471
C. Amphibians . . . . .	475
D. Reptiles . . . . .	476
III. Effects of Reproductive Physiology and Behavior on Stress Responses . . . . .	478
A. Overview of Mammals . . . . .	478
B. Fishes . . . . .	480
C. Amphibians . . . . .	484
D. Reptiles . . . . .	484
IV. The Adaptive Significance of Gonadal-Adrenal Reciprocal Interactions . . . . .	485
V. Future Research Directions . . . . .	488
VI. Acknowledgments . . . . .	489
VII. References . . . . .	489

CHAPTER 17

REGULATION OF REPRODUCTIVE BEHAVIORS

Frank L. Moore

I. Female Reproductive Behaviors . . . . .	506
A. Teleostean Fishes: Females . . . . .	506
1. Sexual Attractivity . . . . .	506
2. Proceptive and Receptive Behaviors . . . . .	507
B. Amphibians: Females . . . . .	508
1. Sexual Attractivity . . . . .	508
2. Proceptive and Receptive Behaviors . . . . .	509

C.	Reptiles: Females . . . . .	509
1.	Sexual Attractivity . . . . .	509
2.	Proceptive and Receptive Behaviors . . . . .	510
II.	Male Reproductive Behaviors . . . . .	511
A.	Teleostean Fishes: Females. . . . .	511
1.	Sexual Attractivity. . . . .	511
2.	Proceptive and Receptive Behaviors . . . . .	511
B.	Amphibians: Males . . . . .	512
1.	Sexual Attractivity. . . . .	512
2.	Proceptive and Receptive Behaviors . . . . .	512
C.	Reptiles: Males . . . . .	514
1.	Sexual Attractivity. . . . .	514
2.	Proceptive and Receptive Behaviors . . . . .	515
III.	Behavioral Activation of Endocrine System . . . . .	515
A.	Fishes: Behavioral Activation . . . . .	515
B.	Amphibians: Behavioral Activation . . . . .	516
C.	Reptiles: Behavioral Activation . . . . .	516
IV.	Summary and Future Research . . . . .	517
V.	References . . . . .	518

CHAPTER 18

THE EVOLUTION OF VIVIPARITY IN FISHES, AMPHIBIANS AND REPTILES:  
AN ENDOCRINE APPROACH

Louis J. Guillette, Jr.

I.	Introduction and Terminology. . . . .	523
II.	Viviparity in Fishes, Amphibians and Reptiles. . . . .	524
III.	Gestation Maintenance and Early Placentation . . . . .	527
A.	Chondrichthyan Fishes. . . . .	527
1.	Previous Research. . . . .	527
2.	Future Research Needs. . . . .	529
B.	Bony Fishes. . . . .	530
1.	Previous Research. . . . .	530
2.	Future Research Needs. . . . .	533
C.	Amphibians . . . . .	534
1.	Previous Research. . . . .	534
2.	Future Research Needs. . . . .	540
D.	Reptiles . . . . .	542
1.	Previous Research. . . . .	542
2.	Future Research Needs. . . . .	550
IV.	Acknowledgments. . . . .	552
V.	References . . . . .	552

CHAPTER 19

AGING OF THE NEUROENDOCRINE SYSTEM

Martin P. Schreibman, Henrietta Margolis-Nunno,  
and Leslie Halpern-Sebold

I.	Introduction . . . . .	563
A.	Background . . . . .	563
B.	The Platyfish ( <u>Xiphophorus maculatus</u> ; Poeciliidae): A Model to Study Aging . . . . .	564
II.	Brain. . . . .	565
A.	Birth to Sexual Maturity . . . . .	565
1.	Gonadotropin-releasing Hormone (GnRH). . . . .	565
B.	Maturity to Senescence (8 to 30 months). . . . .	567
1.	GnRH in NOR. . . . .	567
2.	GnRH in NPP. . . . .	568
3.	GnRH in NLT. . . . .	569
4.	Serotonin (5HT). . . . .	569
5.	Tyrosine Hydroxylase (TH). . . . .	571
III.	Pituitary Gland. . . . .	571
A.	Birth to Sexual Maturity . . . . .	571
1.	Gn and GnRH. . . . .	571
B.	Maturity to Senescence . . . . .	572
1.	Gn and GnRH: Ventral CPD. . . . .	572
2.	Gn and GnRH: Pars Intermedia. . . . .	572
3.	Serotonin. . . . .	573
4.	Tyrosine Hydroxylase . . . . .	573
IV.	Gonads . . . . .	574
A.	Birth to Sexual Maturity . . . . .	574
1.	Testis . . . . .	574
2.	Ovary. . . . .	574
B.	Maturity to Senescence . . . . .	574
1.	Testis . . . . .	574
2.	Ovary. . . . .	576
V.	Synthesis, Summary and Suggestions for Future Research Directions . . . . .	576
VI.	Acknowledgments. . . . .	580
VII.	References . . . . .	581
	CONTRIBUTORS . . . . .	585
	SPECIES INDEX . . . . .	589
	SUBJECT INDEX . . . . .	595