

Contents

1 Birds' Eye Views	1
1.1 Metaphor and Reality	1
1.2 Many Birds, Many Views	3
1.3 The Tuning of Senses	6
1.4 Epicurus, Sextus, and the Sceptics	9
1.5 Sensory Ecology	11
 2 Vision	 19
2.1 The Emergence of Vision	19
2.2 What Eyes Do	21
2.3 Optimal Eyes	22
2.4 A Fundamental Trade-off in Vision	24
2.5 The Primacy of Vision in Birds	27
2.6 Sources of Variation in Camera Eyes	28
2.6.1 <i>The Basic Functional Components</i>	28
2.6.2 <i>Optical Systems of Camera Eyes</i>	31
2.6.3 <i>The Image-analysing System</i>	33
Colour vision and sensitivity in the spectrum	34
Photoreceptors and visual pigments	36
2.7 Variation of Image Analysis	40
2.7.1 <i>Variations in the Distributions of Receptors in a Single Eye</i>	43
2.8 Variation of Optical Structure	49
2.9 Variation of Visual Fields	55
2.10 Comparing Doves and Shearwaters: An Example of the Visual Ecology of Optical and Retinal Structures	57
2.11 Measures of Spatial Resolution	58
2.11.1 <i>Acuity</i>	58
2.11.2 <i>Contrast Sensitivity</i>	61
2.12 Conclusion: Vision in Birds	62

3 Hearing and Olfaction	65
3.1 Hearing	66
3.1.1 <i>The Sound Stimulus</i>	68
3.1.2 <i>The Hearing System of Birds</i>	69
3.1.3 <i>Hearing Sensitivity</i>	70
3.1.4 <i>Locating Sounds</i>	73
Determination of sound direction	73
Determination of sound distance (sound ranging)	77
3.1.5 <i>Echolocation (active SONAR)</i>	78
3.1.6 <i>Conclusion: Hearing in Birds</i>	82
3.2 Olfaction	83
3.2.1 <i>Organization of the Olfactory Systems of Birds</i>	84
3.2.2 <i>The Importance of Olfaction and Olfactory Bulb Size</i>	86
3.2.3 <i>Olfactory Information and Foraging for Specific Items</i>	86
3.2.4 <i>Detection of Foraging Locations using Olfaction</i>	87
3.2.5 <i>Body Odours and Semiochemicals</i>	89
Odour-based recognition of species	89
Odour-based recognition of individuals	90
Odour-based recognition of individual quality and mate choice	90
3.2.6 <i>Odours and Nests</i>	91
3.2.7 <i>Conclusion: Smell in Birds</i>	92
4 Touch, Taste, and Magnetoreception	94
4.1 Touch or Somatic Sensitivity	94
4.1.1 <i>Somatic Sensitivities</i>	96
Mechanoreception	96
<i>Herbst corpuscles</i>	96
<i>Grandry corpuscles</i>	97
<i>Thermo-sensitive receptors</i>	97
<i>Cutaneous nociceptors</i>	98
4.1.2 <i>Bill Tip Organs</i>	98
Bill tip organs in waterfowl	98
Bill tip organs in parrots	99
Bill tip organs in shorebirds, kiwi, and ibises	101
4.1.3 <i>Conclusion: Somatic Sensitivity in Birds</i>	103
4.2 Taste	103
4.2.1 <i>Taste Buds</i>	104
4.2.2 <i>Taste Genes and Taste Receptors</i>	104
4.2.3 <i>Relative Numbers of Taste Receptors</i>	105
4.2.4 <i>Taste Categories in Birds</i>	105
Sweet	105
Umami	106
Bitter	106
Calcium	106
Salt	106

Sour	107
Fat	107
4.2.5 <i>Taste and Foraging in Shorebirds</i>	107
4.2.6 <i>Conclusion: Taste in Birds</i>	108
4.3 Magnetoreception	108
4.3.1 <i>Animals that Detect the Geomagnetic Field</i>	109
4.3.2 <i>Magnetic Compass Mechanisms</i>	110
4.3.3 <i>Detection of the Geomagnetic Field</i>	110
The magnetite model of magnetic field detection	110
The radical pair model	111
4.4 Conclusion: Magnetoreception in Birds	112
 5 From Senses to Sensory Ecology	 114
5.1 Making Sense of the Diversity of Bird Senses	114
 6 Birds in the Dark: Complementary and Partial Information	 117
6.1 The Problem of Night-time	119
6.2 Absolute Visual Sensitivity and the Challenges of the Nocturnal Environment	125
6.3 Visual Sensitivity in Context: In and Out of the Woods	126
6.4 Nocturnal Birds	127
6.5 The Owls' Solutions to Nocturnality	128
6.6 The Oilbirds' Solution to Nocturnality	132
6.7 The Kiwi's Solution to Nocturnality	134
6.8 Nocturnality in Other Birds	141
6.8.1 <i>Nocturnal Parrots</i>	141
6.8.2 <i>Nightjars, Frogmouths, and Potoos</i>	145
Nightjars	145
Frogmouths and Potoos	149
6.9 Occasional Nocturnality	151
6.9.1 <i>Occasional Nocturnal Foraging</i>	151
6.9.2 <i>Nocturnal Migration</i>	156
6.9.3 <i>Night Attendance at Nests</i>	158
6.10 Conclusion: Birds in the Dark—Complementary and Partial Information	159
 7 Birds Underwater: A Paucity of Information	 161
7.1 The Underwater Foragers	162
7.2 Optical Challenges of Foraging Underwater	163
7.3 Light Levels and Spectral Challenges of Foraging Underwater	166

7.4	The Challenge of Rapidly Changing Light Levels	168
7.5	Aquatic Foraging and Nocturnal Foraging	169
7.6	Tactile Information and Underwater Foraging	170
7.7	Solutions to Underwater Foraging	172
7.7.1	<i>Cormorants</i>	174
7.7.2	<i>Penguins</i>	178
7.7.3	<i>Auks</i>	180
7.8	Birds Underwater: A Paucity of Information	181
8	What Drives Bird Senses?	183
8.1	Visual Ecology, Trade-offs, and 'Just-so Stories'	185
8.2	Which Tasks Drive the Evolution of Sensory Systems in Birds?	186
8.2.1	<i>Key Tasks and Perceptual Challenges Faced by Birds</i>	187
	Flight	187
	Foraging	188
	Predator detection	189
	Reproduction	189
8.3	Competing Tasks and Competing Information	190
8.4	General Characteristics of the Visual Fields of Birds	191
8.5	Functional Interpretations of the Visual Fields of Birds	194
8.6	The Key Functions of Bird Visual Fields	194
8.6.1	<i>Control of Bill Position in Foraging</i>	194
8.6.2	<i>Panoramic Vision</i>	195
8.6.3	<i>Differences in Visual Fields between Closely Related Species</i>	196
8.6.4	<i>The Perceptual Demands of Bill Control versus Predator Detection</i>	196
8.7	What Is the Function of Binocular Vision in Birds?	198
8.7.1	<i>Binocular Vision in Birds</i>	198
	Binocular field width	200
	Vertical extent of binocular fields	201
	Abolishing binocular vision	202
	Binocular field widths, nocturnality, and predation	204
8.8	Visual Fields, Eye Size, and Imaging the Sun	207
8.9	Summary: The Key Drivers of Visual Fields in Birds	209
8.10	Binocular Vision, Optic Flow-fields, and Contralateral Vision	210
8.11	Summary: The Drivers of Visual Fields and their Fine Tuning	212
8.12	What Drives Colour Vision in Birds?	213
8.13	What Drives Bird Senses?	215
9	The Sensory Ecology of Collisions and Entrapment	217
9.1	Why Do Flying Birds Collide with Static Objects?	219

9.2	Information Available to Flying Birds	220
9.2.1	Colour Vision	220
9.2.2	Spatial Resolution	220
9.2.3	Relative Depth, Distance, and Time-to-contact	221
9.2.4	Fields of View	222
9.3	Comparing Bird and Human Views of their Worlds	222
9.4	The Functions of Lateral Vision in Birds	223
9.5	When Birds are Flying in Open Airspace, What are they Doing?	224
9.5.1	Looking but Failing to See	224
9.5.2	Can Flying Birds Adjust their Rate of Gain of Visual Information?	225
9.5.3	Are Flying Birds Always Looking Ahead?	226
9.6	The Sensory Ecology of Collisions	227
9.7	A Sensory Ecology Perspective on Collision Mitigation	229
9.7.1	Collisions with Static Hazards	229
	Visual factors	231
	Perceptual factors	232
	Diverting and distracting birds	232
	Tailored rather than general solutions	233
9.7.2	Collisions with Moving Hazards: Aircraft and Wheeled Vehicles	233
	Manipulating the environment	233
	Manipulating the hazard	234
	Are vehicles perceived as predators?	234
9.8	Entrapment: The Problem of Gillnets and Diving Birds	235
9.9	Gillnet Bycatch Bird Species	235
9.10	The Role of Vision in Seabird Gillnet Bycatch Species	236
9.11	Distracting Birds from Nets	237
9.12	A Sensory Ecology Solution to Gillnet Bycatch?	237
9.12.1	Making Nets Conspicuous	237
	Lighting nets	238
	Warning birds of the presence of nets	238
9.13	Warning Panels	239
9.13.1	Patterns on Warning Panels	239
9.13.2	The Size of Warning Panels	239
9.13.3	The Colour of Warning Panels	240
9.13.4	The Detection Distances of Warning Panels	240
9.13.5	How Many Panels?	240
9.13.6	Would Warning Panels Be Effective?	241
9.14	Collisions with Glass	241
9.14.1	Mitigation Measures	241
	Patterns on glass surfaces	242
	UV patterns on glass	242
9.15	The Sensory Ecology of Collisions and Entrapment: Conclusions	243

10 Postscript: Conclusions, Implications, and Comment 244

Appendix 1	247
Appendix 2	253
References	259
Index	287