

CONTENTS

<i>List of Plates</i>	vii
<i>Foreword</i>	ix
<i>Acknowledgments</i>	xiii
1 Introduction	1
2 Natural History, Systematics, and Phylogenetics	4
3 Development	23
4 Anatomy and Physiology	47
5 Genetics and Genomics	76
6 Neurobiology	90
7 Neuroethology and Cognitive Science	116
8 Reproduction	137
9 Evolution	159
10 Life History, Ecology, and Nesting Biology	182
11 The Honey Bee Colony Is a Superorganism	196
12 Division of Labor	204
13 Communication, Labor Allocation, and Collective Decision Making	226
14 Chemical Ecology	250

vi CONTENTS

15	Foraging	272
16	Tropical Honey Bees	290
17	Immunity, Parasites, Pests, and Pathogens	301
18	Detoxification and Pesticides	322
19	Honey Bees as Managed Pollinators	338
	<i>Literature Cited</i>	353
	<i>Index</i>	477

1

Introduction

Honey bee biology does not need much selling to attract the nontechnical reader, or the applied scientist working in agriculture. But are honey bees as interesting and important for basic scientists? The answer is yes. The honey bee is in fact one of the best-understood organisms from an integrative biology perspective. A search of any scientific search engine, for example, will locate thousands of papers about honey bee biology. The majority of these are not about agriculture, or any aspect of applied bee biology, but rather focus on the basic science of bees. Studies of their systems of communication, the developmental mechanisms leading to queen versus worker morphology, and division of labor, for example, have vast bodies of work.

This fascination with bees might need some explaining. Of course, model systems in biology, like the fruit fly, are the subject of many more studies than are honey bees. However, the fruit fly is a model for genetics, and the overwhelming majority of fruit fly studies are about that subject. There is considerable work on other aspects of fruit fly biology, but in general many aspects of their biology are understudied. In a sense, this is because these animals serve as medical models that we use to address biological questions of practical concern. This is generally the case for model systems.

In contrast to the model systems, the honey bee, until recently, was studied by biologists mainly because it is interesting and because we like bees. In other words, science simply for the sake of knowledge drives quite a lot of honey bee biology. Because of this, we know a great deal about every aspect of bee biology, both at the molecular and the organismal levels. This is not to say that the honey bee is not a model, as well, for some questions. The honey bee is in fact something of a model system for social insect biology. Social insects are the most complex animal societies, and they are ecologically dominant in many habitats. Among the social insects, the honey bees are not the most complex,

but they are the most amenable to study. The long history of beekeeping, which provides many tools for the scientist, ensures that they are easier to work with than insects with no history of management. Hence, researchers interested in social behavior, pollination, communication, and many other topics naturally gravitate to the honey bee as a subject organism.

Having covered in broad strokes why the honey bee attracts so much attention, we now turn to the other major question of the introduction. Why this book and why now? The answer is simple. There is a wonderful reference for the basic biology of the honey bee, Mark Winston's *The Biology of the Honey Bee*. This has long been on the shelves of scientists interested in bees. Beekeepers interested in acquiring a deeper understanding of the creatures they love have also made much use of this work. However, Winston's book is now over 30 years old and is out of date on many subjects. It is chiefly lacking in two ways. First, many of the subjects covered in the Winston book have changed radically in scope, with major new approaches having uncovered phenomena unknown when that book was published. Second, there are now several fields in biology that, although present 30 years ago, were little studied, and hence did not get covered in Winston's book. Some of these fields are now larger than some traditional fields; examples include toxicology, pollination, and immunity. Hence, the goal of this book is to provide a new standard reference for honey bee biology that explores this fascinating insect from both traditional and new scientific perspectives.

To the Beekeeper

This is a book for scientists about the biology of honey bees, so one might be surprised to find a section addressed to beekeepers. The surprised person would not be too familiar with beekeepers, however, since this group of enthusiasts is so fascinated by the colonies they care for that they routinely buy books such as this and invite practicing scientists to talk at their beekeeping clubs. I personally have seen the Winston book in the hands of many beekeepers. Hence, I want to provide a brief guide to reading this book for the nonscientist.

In general, any topic that does not take a molecular approach should be approachable for a beekeeper. This includes most of the work on anatomy and physiology, taxonomy, reproduction, neuroethology, division of labor, task allocation, chemical communication, nesting biology, parasites and pathogens, tropical bees, and pollination. These are the topics typically of most in-

terest to beekeepers. Although there is some molecular biology in these sections, it is not central to understanding the science. The chapters on development, evolution, genetics, and neurobiology, in contrast, are probably too technical for the lay reader. However, I think with some determination the beekeeper could grasp the key ideas even in these chapters. I say this because there are now so many free sources of information to get a better understanding of background material. I imagine with some background reading, and maybe viewing of some science tutorials on YouTube, that quite a lot of the technical material might become transparent.

INDEX

- absconding, 20, 295–296
adjuvants, 333–334
African bees, 15, 18, 157, 170, 184, 292, 296–297
Africanized bees: beekeeping and, 300, 344; biology of, 297–300; defensive behavior of, 291–293; genomics of, 170; interspecific competition and, 187; kin selection studies of, 166; nesting, 291; population biology of, 184; QTL studies in, 83–84; *Varroa* resistance of, 293–295
afterswarms, 139–141
aggression, Africanized versus European bees, 292; against beekeepers, 190–191; genetic basis of, 84, 114; in nestmate recognition, 269
alarm pheromone, 190, 242, 252, 266–267, 293
American foulbrood, 85, 148, 314–316
anarchistic bees, 158, 261
antenna, 48–50, 53, 63, 66, 94–96, 103, 115, 122, 220, 248, 252
antennal lobes: biogenic amines and, 216, 220; development of, 115; spatial processing in, 96–98; structure of, 91
antimicrobial peptides, 213, 302–305, 329, 351
Apis andreniformis, 11
Apis cerana, 12
Apis dorsata, 11–12
Apis florea, 11
Apis laboriosa, 11–12
Apis mellifera: domestication of, 18–22; evolutionary origin of, 16–18; genome of, 88–89; geographic range of, 12; GWAS studies in, 86; management of, 20–21; predators of, 190; subspecies of, 10–11, 13–16, 169–170; wild populations of, 18–19, 185
auditory processing, 95
bee bread, 66–68, 205, 209, 329–330, 349
beekeeping, artificial selection and, 19–20; commercial, 343–344; Darwinian, 312; domestication, 18–22; history of, 2; queenlessness and, 144; small hive beetle and, 314; supersedure and, 143; wax moths and, 314
Bombus, 171–172, 173, 180, 187, 324
brain: biogenic amines and, 216, 218–222; development, 37, 42, 150–151, 213; distributed physiology and, 202; endocrine system and, 62; gene expression in, 152, 173, 175; methylation of, 44; QMP and, 155; structure, 90–92
brood food, 34, 52, 177, 208, 213, 252, 264; nutritional content, 68–69
brood pheromone, 214, 223, 225, 242, 253–254, 255, 260, 262, 264, 279, 288
buzz run signal, 233, 246
caffeine, 327
capping cells, 39, 208, 262, 314
carbon dioxide, 248–249
caste determination: 36–46, epigenetics of, 37, 43–46; hormonal control of, 39–42, insulin signaling and, 42–43; role of microRNAs in, 37; role of sugars in, 36–37

- chalkbrood, 148–149, 307–308, 316–317
- circadian rhythm: behavioral studies of, 133;
molecular genetics of, 110–112, 133–136;
neurobiology of, 112–113
- circulatory system, 61
- cocoon, 34, 39–40, 192, 208
- colony collapse disorder, 317, 319, 329, 338,
344–345
- collective decision making, 277–278; nectar
foraging, 272–275; nest choosing,
243–249; self-organization and,
239–240
- comb, pattern formation on, 239–240
- compound eyes, 49–50, 105
- corpora allata, 62
- corpora cardiaca, 62
- crop, 55–56, 67, 71, 73–74, 92, 265, 273, 297
- deformed wing virus, 308, 310–311, 313,
318, 320, 321
- detoxification systems, 323–328
- digestive system, 55–56
- distributed Physiology, 202–203
- division of labor: Africanized versus Euro-
pean bees, 291; biogenetic amines and,
216–220; genetic basis of, 220–225;
physiological specialization associated
with, 211–213; reproductive, 204–205; in
workers, 205–210
- drone congregation areas, 145, 256–257
- drones: accessory glands of, 152–153;
anatomy and physiology, 65–66; rearing
of, 142–143; reproductive behavior of,
151–152
- (E)-10-hydroxy-2-decenoic acid (10-HDA),
38, 44, 252, 257
- eggs, 23–24
- embryogenesis, 24–29
- endocrine system, 39–40, 61–63, 91, 92,
113, 202
- essential amino acids, 67
- essential fatty acids, 68
- European foulbrood, 316
- eusociality: evolution of, 171–175; grades
of, 9
- evo-devo, 25–28
- excretion, 323
- exoskeleton, 60–61
- fanning, 205, 264; temperature control,
236–237, 248–249; ventilation, 249
- fat body, 56, 59, 150, 176, 193, 220, 309;
division of labor and, 213–215
- flight muscles, 55, 92, 232, 247–248, 284, 339
- foragers: assessment of patch quality,
276–277; improvement with experience,
284–286; nectar, 272–275; pollen,
276–282; role of octopamine, 217–218;
water collection by, 282
- genomic imprinting, 165–167
- germ cell differentiation, 29
- glands: Dufour's gland, 58–60, 64, 143, 151,
223, 257–258, 261–262, 270; hypophar-
ryngeal, 36, 51–52, 60, 68–69, 72–73,
175, 180, 208, 257, 264, 270, 304, 329;
Koschevnikov, 58, 60, 266; mandibular,
36, 51–52, 68, 141, 150–151, 154, 208,
213–214, 223, 256–258, 261, 265, 270,
304, 329; Nasonov, 59–60, 150, 252,
257, 264–265; salivary, 34, 52–53,
60, 91, 257, 270–271; venom, 58, 153,
176, 181, 257; wax, 59–60, 192–193,
209, 257
- grooming invitation signal, 231–232
- growth rate: Africanized versus European
colonies, 290
- guarding, 178, 191, 205, 209, 214, 242;
robbing and, 188–189; specialization
and, 235–236
- gustation, 103–104
- haplodiploidy, 23, 29, 87
- head, 48
- hemolymph, 56–57
- heritability, 78
- honey, 66–67

- Hox genes, 25–28
- hygienic behavior: Africanized bees and, 294; American foulbrood and, 316–317; caste and, 205, 209, 306; diseases resistance and, 307–308; genetic basis of, 84–86
- imaginal discs, 34
- immune system, 301–304
- insulin signaling, 39–40, 42, 83, 170, 220–221
- intercaste, 38–39
- interspecific competition, 185–187
- invertase, 67
- Israeli acute paralysis virus, 304, 306, 319–321
- Johnstone’s organ, 94
- juvenile hormone: caste differentiation and, 39–42; circadian rhythm and, 133; corpora allata and, 62; division of labor and, 177–178, 213–217, 222–223, 264; drones and, 152; laying workers and, 154; neurogenomics and, 113; queen reproduction and, 150–151; task allocation and, 139
- kin recognition, 201
- kin selection, 159–168
- Kruppel homolog, 223–224
- Langstroth hive, 19–20, 194
- larvae, 33–34
- laying workers, 65, 154–157, 164–165
- learning: aversive, 219; caffeine and, 327; fatty acids and, 68; foraging and, 285; mushroom bodies and, 91, 97; olfactory, 98–102, 121–124; orientation and, 125, 128–130; pesticides and, 331–333; visual, 119–121, 232, 261
- legs, 24, 53–54, 91–92, 103, 145, 193
- life cycle, 9, 154, 182
- lifespan: Africanized versus European, 290
- local adaptation, 169–170
- magnetic sense, 136
- major royal jelly proteins, 69, 89, 180–181
- Malpighian tubules, 56, 224
- mating, 19, 66, 145–147, 150–151, 256–257
- mating flights, 132, 143–144, 147, 149–152
- mechanical senses, 93–95
- Melipona, 8
- memory: caffeine and, 327; mushroom bodies and, 91, 97; olfactory, 102–104, 114; pesticides and, 330–331, 333; visual, 121, 128
- Mendelian traits, 76–77
- mesosoma, 48, 53–55
- messenger bees, 205, 208, 252, 258, 263
- metasoma, 48, 55–60
- microbiome, function of, 73–75; larval, 70; queen and drone, 72; worker, 70–72
- middle-age bees, 200, 208, 217, 235, 240–248; caste and, 205–207; collective foraging and, 272–273; comb building and, 192–194; endocrine control of, 213–214; task repertoires of, 209–210
- migratory behavior, 296–297
- modulatory signaling, 233–235
- molting, 33–34, 39, 42, 61–62
- mouthparts: 50–52
- mushroom bodies, 91, 97, 99–102, 107, 114, 150, 218
- navigation, cognitive map, 130–132; image matching, 128–130
- nectar, 67, digestive processing of, 67; toxic sources, 69–70
- nectar guide, 119
- neonicotinoids, 322, 325–328, 329, 331, 335–337, 349, 351
- nest: Africanized versus European bees, 291; characteristics of, 191–192; finding a new, 243–246
- nestmate recognition, 189, 218, 268–271
- neurosecretory cells, 62
- newly emerged bees, 70, 74–75, 208, 268, 286, 310, 318
- nicotine, 326

- Nosema, 304, 317, 319, 321, 350–351
- nurses, 33, 34, 36, 52, 72, 112, 115, 151, 193, 212, 213, 240, 241, 279, 305, 316, 319;
brood food and, 68–69; caste determination and, 38–39; circadian rhythm and, 133–135; division of labor and, 205–209; dopamine and, 218–220; juvenile hormone and, 214–216; microbiome and, 70–71; pheromones and, 223, 225, 264–265; reverted, 210–211; Varroa and, 309–310; vitellogenin and 177–178, 309–310
- nutrition, 66–70, 349
- ocelli, 50–51, 104
- olfaction: discrimination and resolution, 123–124; learning, 98–101; neuroanatomy of, 95–97
- ommatidia, 105–106, 117–118, 129
- optic flow, 126–128
- orchid bees, 8
- orientation flights, 124–125, 132, 150, 151
- ovaries, 41, 42, 44, 144, 158, 166, 176, 256;
anatomy of, 64–65; laying workers and, 153–156, 164–165, 259–261; reproductive physiology and, 150–151
- pars intercerebralis, 222
- parthenogenesis, 16, 156–158
- path integration, 125–128, 130, 132
- patrolling, 194, 205, 207, 234, 240–242, 279
- pattern formation: comb, 239–241
- pesticides: in the comb, 329–330; interactions with other pesticides, interactions with other stressors, 350–351; 334–335; sublethal effects and, 330–333, 335–337
- piping: in nesting finding, 245; queen, 233; worker, 232
- polarized light, 105, 118, 126
- pollen basket, 8, 38, 53, 63, 65
- pollen hoarding bees, 80–84
- pollination: basic biology of, 338–340; honey bees and, 341–344
- polyandry: disease resistance and, 148; evolution of, 147–149; patriline consequences of, 77–78; task allocation and, 237–239; worker policing and, 160
- population biology, 184–185, 290, 345–348
- precocious foragers, 115, 133, 177, 210–211, 212, 213, 216, 220–221
- prepupae, 7, 34, 40–41
- proporoboscis extension reflex (PER), 83, 96, 122–124
- propolis, 53, 73, 193, 194–195, 205, 209, 210, 303, 306, 315, 325
- pupae, 34–35, 304, 306, 310, 319
- QTL mapping, 78–86, 158, 292, 313
- queen cups, 139, 143–144, 192, 263–264
- queen duels: behaving during, 141–142; kin selection explanation for, 162–163
- queen mandibular gland pheromone (QMP): anarchistic bees and, 158; glandular source of, 256–258; laying workers and, 154–155; as passenger pheromone, 251–252; and retinue response, 258–259; role in division of labor, 214–215, 218–220, 223, 225, 264; and sexual attraction, 257; suppression of workers ovaries, 260; and swarming, 262–264
- queenless colonies, 24, 144, 160, 232, 258; reproduction in, 154–155, 260–261; selfish workers and, 164–165
- queens: caste determination and, 36–46; egg laying, 23–24; growth as larvae, 33–34; mating, 19, 132; morphological differences relative to workers, 63–65; ovary suppression of workers by, 259–260; pheromones, 52, 60, 141; reproductive physiology, 66, 150–151; reproductive system, 64; sex determination and, 32–33; subspecies variation in, 13; virgin behavior of, 149–150
- recombination, 87–88, 157
- rectum, 56, 71
- reverted nurses, 133, 210–211, 216
- robbing, 187–189

- royal jelly: microbiome and, 73; nutritional content of, 68–69; pheromones and, 252; role in caste determination, 36–46
- scouts, 114, 139, 174, 188, 205, 233, 238, 243–246, 273–275, 277–278, 297
- self-organization, 239–243
- sex determination: molecular genetics of, 30–33; population genetics of, 168–169
- shaking signal, 139, 205, 228, 231, 234, 275
- small hive beetle, 314–315
- social anatomy, 198
- social detoxification, 329
- social hormones, 254
- social immunity, 306–307
- social physiology, 198–199
- solitary bees, 4, 6, 187, 202, 277, 320, 342
- spermatheca, 64–65, 146–147
- spermatogenesis: 29
- stimulus response thresholds, 78, 235–237, 286–289
- stinger, 38, 57–59, 63–64, 190
- stingless bees, 5, 8, 10, 51, 147, 342
- stop signal, 227, 228, 232, 246
- subgenual organ, 53, 94
- sun compass, 117, 126, 131–132
- supersedure, 143–144, 261–262
- swarming, 10, 149, 154, 182, 210, 228, 232, 233, 246, 261, 284, 295, 297, 312; kin selection and, 163; natural history of, 137–141; pheromonal control of, 262–263; queen duels and, 142; rates, 184
- tarsus, 53
- taxonomically restricted genes, 175–176
- thermoregulation: nest cooling, 248; winter warming, 247–248
- tongue lashing, 205, 209, 248
- trachea, 57, 61–62, 309
- tracheal mites, 309
- tremble dance, 200, 205, 228, 230, 231, 232, 234, 242, 275
- trichoid sensilla, 93–94
- trophallaxis, 50, 205, 206, 208, 279
- ultraspiracle, 214–215
- undertakers, 78, 178, 205, 214, 217, 235, 236, 306
- Varroa mites: Africanized versus European bee resistance to, 293–295, 300; bee declines and, 345, 348, 351; biology of, 309–311; chemical ecology and, 271, 306; DWV and, 311, 318; hygienic behavior and, 307–308; pesticides and, 322, 325, 333; resistance of wild bees to, 311–314; RNAi control of, 320–321; robbing and, 187; wild bees and, 185, 311–314
- venom: queens, 63–64; taxonomically restricted genes, 175; workers, 57–60
- viruses, 317–320
- visceral nervous system, 92
- visual system: acuity of, 117–118; anatomy of, 104–106; color, 107–110, 116; and flowers, 118; polarized light, 126; processing, 106
- vitellogenin, 155, 170, 172, 176–179, 181, 213, 214, 221
- waggle dance: adaptive basis, 283–283; auditory processing, 95; biology of, 229–230; cognitive map and, 131; collective foraging and, 272–274; cues and, 200; genetic variation and, 237; magnetic sense and, 136; migration, 296; nest site selection and, 243–246; optic flow and, 127; pheromones and, 265; recruitment, 281; robbing and, 188; stop signal and, 227, 232; trichoid sensilla and, 6
- wasps, 4, 32, 58, 129, 173, 180, 183, 199–200, 203, 339
- wax, 50, 53, 59–60, 178, 205, 208–209, 235, 248, 257, 273, 306, 314, 315, 333; comb types, 191–192; pesticides and, 329–330; regulation of building, 192–194
- wax moths, 314
- wings, 53–55, 77, 92, 122, 229, 248, 264, 318
- winter bees, 164
- worker policing, 160–162