
History of Ecological Sciences, Part 56: Ethology until 1973

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Introduction

A distinction can be drawn between ecological and psychological studies of animal behavior. The former became ethology and the latter, behaviorism. Robert Boakes, University of Sussex, wrote the history of the latter: *From Darwinism to Behaviourism: Psychology and the Minds of Animals* (1984). However, behavioral psychology is relevant to the study of ethology (Kruuk 2003:3, Burkhardt 2005:8), despite Konrad Lorenz reading works by “Spencer, Lloyd Morgan, MacDougall, Yerkes and Watson” and concluding that “they simply did not know what they were talking about” (quoted in Nisbett 1976:37). While Lorenz’s wholesale dismissal of other approaches and findings than ethological was unfair, his comments illustrate an attitudinal gulf between two different approaches to the study of animal behavior. Yet, zoologists Peter Klopfer and Jack Hailman blended the two approaches in their text, *An Introduction to Animal Behavior: Ethology’s First Century* (1967), as did ethologist Robert Hinde in his *Animal Behaviour: a Synthesis of Ethology and Comparative Psychology* (1970), Michael Fox in his *Readings in Ethology and Comparative Psychology* (1973), and the first two chapters in P. P. G. Bateson and Peter Klopfer’s *Perspectives in Ethology* (volume 1, 1973) are by authors from departments of psychology. American collaborators Vincent G. Dethier, biologist, and Eliot Stellar, physiological psychologist, coauthored *Animal Behavior* (1961, edition 3, 1970), which has six chapters on nervous systems in different kinds of animals and three chapters on behavior, learning, and intelligence. Michael Bright’s *Intelligence in Animals* (1994) is a synthesis of these two approaches for a popular audience.

On the other hand, Lee Drickamer has discussed comparative psychology (example: Maier and Maier 1970), ethology, and ecology as three-fold roots of the study of animal behavior, and he mentioned other investigators’ ways to subdivide these subjects (Vessey and Drickamer 2010, Drickamer 2016). Those various approaches are not discussed here.

There are excellent sources for history of ethology. However, Alfred Espinas’ lengthy “Introduction Historique” to *Des Sociétés Animales* (1878:7–155) has limited interest here, because, rather oddly, it is limited to a survey of ideas on human society (to which he also devoted his final chapter, 458–513, before his conclusions). Psychologist Philip Gray, Montana State University, wrote three historical articles of narrow scope (1962, 1963, 1967), followed by a brief broad historical survey (1968). Thomas McGill, Williams College, compiled a collection of 55 extracts in *Readings in Animal Behavior* McGill (1965) that was topically organized and included two essays on a new science of ethology (Thorpe 1956, Hess 1962). Klopfer and Hailman’s *Introduction to Animal Behavior* (cited above) is not exactly a history of ethology’s first century, but is actually a textbook on ethology written from a historical perspective. G. Richard, Université de Rennes, wrote authoritatively “The Historical Development of Nineteenth and Twentieth Century Studies on the Behavior of Insects” (1973). An attractive, 725-page Grzimek’s *Encyclopedia of Ethology* (1977, German, 1973), contains (English edition) two brief articles on the

history of ethology; neither has references (Burghardt 1977, Heinroth 1977). Nevertheless, Katharina Heinroth's survey should be taken seriously, because it is based upon her own and her late husband, Oskar Heinroth's ethological knowledge. Konrad Lorenz wrote a historical introduction to his *Foundations of Ethology* (1981:1–12, German, 1978), which included history of his own studies. Cambridge University ethologist William Thorpe wrote a concise *The Origins and Rise of Ethology* (1979), which included references and brief account of his own work. John Durant wrote "Innate Character in Animals and Man: a Perspective on the Origins of Ethology" (1981), with references.

Bernard Singer's "History of the Study of Animal Behaviour" (1982) is the only history I know that seriously surveys from antiquity to recent times. His slight confusion concerning Réaumur's publications and an incorrect date for Gray 1968 are minor errors, but documentation for his article is limited. Gordon Burghardt compiled *Foundations of Comparative Ethology* (1985) that contains extracts from 1835 to 1937. F. M. Scudo discussed aspects of history in "'Ethology,' 'Ecology,' and 'Philosophy'" Scudo (1989). Unique resources are two volumes of autobiographical essays: *Studying Animal Behavior: Autobiographies of the Founders* (Dewsbury 1985) and *Leaders in Animal Behavior: The Second Generation* (Drickamer and Dewsbury 2009). Irenäus Eibl-Eibesfeldt, author of an ethology textbook (1970), earlier published, with Sol Kramer, an essay explaining this new science (1958). Feminist historian of biology Donna Haraway published a detailed *Primate Visions: Gender, Race, and Nature in the World of Modern Science*, beginning in 1908 (1989), and Georgina Montgomery published a less ideological study than Haraway's: *Primates in the Real World: Escaping Primate Folklore and Creating Primate Science* (2015). In 1989, the American Society of Zoologists celebrated its centennial with six papers in a Symposium on "Animal Behavior: Past, Present, and Future," which appeared in *American Zoologist* (1991). Lynne Houck and Lee Drickamer edited a more chronologically broad collection than McGill's: *Foundations of Animal Behavior: Classic Papers with Commentaries* (1996), which included works from 1872 to 1973. Their *Foundations* is divided into six parts, and each part has a historical introduction by a different investigator. John Clark's "Ethology and animal behavior" (2000) is a bibliographical essay that cited and critically discussed 17 publications.

There are excellent detailed biographies of the two most important founders of ethology, both well illustrated: Klaus Taschwer and Benedick Föger, *Konrad Lorenz: Biographie* (2003), and Hans Kruuk, *Niko's Nature: The Life of Niko Tinbergen and His Science of Animal Behaviour* (2003). Two years later, Richard Burkhardt, Jr. published, also in great detail, *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology* (2005), which is broader in timespan than the title indicates. Lee Alan Dugatkin, like Eibl-Eibesfeldt, has published both a textbook (2004, edition 2, 2009b) and a historical study: *The Altruism Equation: Seven Scientists Search for the Origins of Goodness* (2006). His textbook contains interviews with 17 ethologists. Dale Peterson's lengthy biography of Jane Goodall (2006) includes details on the history of ethology, particularly in relation to primates. Tim Birkhead, Jo Wimpenny, and Bob Montgomerie's *Ten Thousand Birds: Ornithology since Darwin* (2014) has three relevant chapters: "Ecological Adaptations for Breeding," "The Study of Instinct" and "Behavior as Adaptation." *A Journal of the History of the Behavioral Sciences* began in 1965. The series, *Perspectives in Ethology*, edited by P. P. Bateson and P. H. Klopfer (vol. 1, 1973, vol. 2, 1976, etc.), is not historically oriented, but as time goes by, early volumes become of historical interest. Other historical articles are cited below.

This survey is selective; the 19 autobiographical essays collected by Dewsbury in *Leaders in the Study of Animal Behavior* (1985), are from investigators who had made substantial contributions by

1973. English ethologist William H. Thorpe (1902–86) was likely invited to submit an autobiographical essay (to make a total of 20), but perhaps he was unable to write one, due to declining health (Gillespie 1990, Costall 2004). He had briefly summarized his own work in his *Origins and Rise of Ethology* (1979:118–123). Some autobiographical essays collected by Drickamer and Dewsbury, *Leaders in Animal Behavior: The Second Generation* (2010) also include noteworthy contributors active before 1973.

There are at least three dictionaries of ethology. One, edited by Harré and Lamb (1986) has entries by 46 authors that include historical information and bibliographies. The dictionary by Immelmann and Beer (1989) is mostly a translation of Immelmann's *Wörterbuch der Verhaltensforschung* (edition 3, 1982). Edward Barrows' *Animal Behavior Desk Reference: A Dictionary of Animal Behavior, Ecology, and Evolution* (1995, edition 3, 2011) is the most detailed, with historical references and bibliography.

With abundant historical resources, I have been selective rather than comprehensive. My end-date of 1973 is based upon the award of a Nobel Prize in 1973 to Frisch, Lorenz, and Tinbergen, which brought ethology from the periphery into mainstream biology and ecology. Conveniently, Hinde's *Animal Behaviour* (1970) and Irenäus Eibl-Eibesfeld's textbook, *Ethology: the Biology of Behavior* (1970) summarized much of what ethologists had achieved by then; the National Geographic Society published a well-illustrated, popular survey of *The Marvels of Animal Behavior* (Allen 1972) by 22 authors (all academics), and the 41 chapters in Grzimek's *Encyclopedia of Ethnology* (Immelmann 1977:725, German, 1973) provided broad surveys of ethology around the same time (Fig. 1).

Natural history

The most important early source for ethology was natural history literature, and in W. H. Thorpe's conception of ethology, its contributions followed “three scientific ways of probing into the behavior of animals” (1956, reprinted 1965:35), the ways of naturalists, psychologists, and physiologists.

Scientific natural history began at Aristotle's Lyceum in Athens in the later 300s BC, when zoology and botany were founded. How many reported observations were made by Aristotle, if any, is unclear, but he may have been involved in organizing and interpreting information collected. Besides literature on Aristotle as an ecologist (Bodenheimer 1954, Egerton 1975, 2001a, 2012:4–7, Birkhead 2008:see index), there are at least six articles on his ethology, plus brief discussions by Heinroth (1977:1), Singer (1982:259–261), and Lindauer 1985:129). Two articles were stimulated by Karl von Frisch's accounts of hive bee communication: Kraak (1953) discovered a passage in *Historia Animalium*, book 9, 624b about the bees' dance, and Haldane (1955) appreciated Kraak's discovery, but disliked his translation of the passage and offered his own, which is satisfactory, but here is a professional translator's version (Aristotle 1991:343):

On each flight the bee does not go on to flowers different in form; it goes for example from violet to violet, and does not touch any other before it has flown back to the hive. And having arrived at the hive they shake themselves, and three or four bees attend to each. What they pick up is not easy to see, nor has there method of working it been seen...

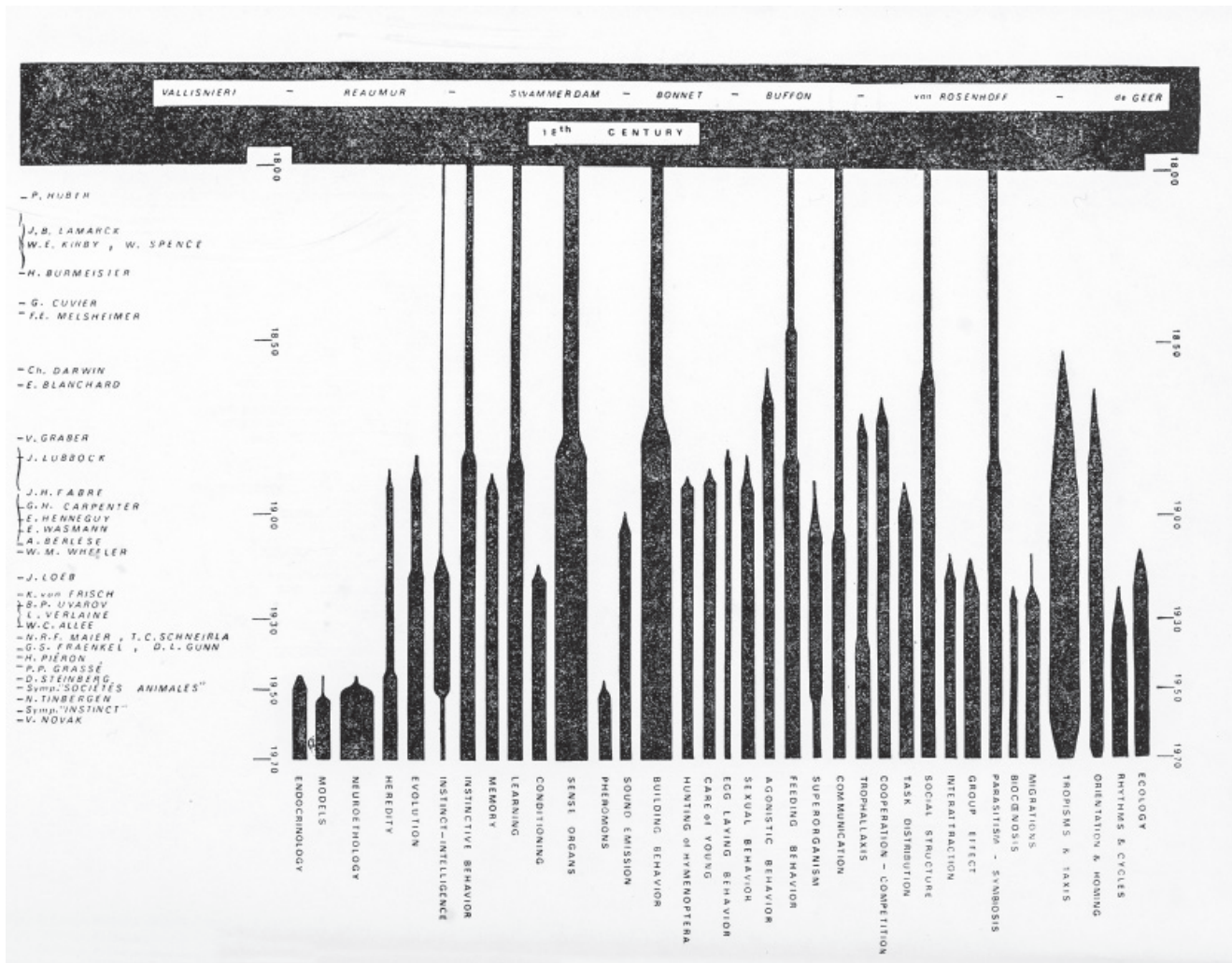


Fig. 1. Origin and importance of major behavioral research on insects during the 1800s and most of the 1900s. Authors are indicated when their first fundamental publication appeared. This chart emphasized continuity between the natural history and ethology periods. Richard 1973:480.

That is, the dance was discovered in antiquity, but not its purpose. Jean-Louis Labarrière wrote a detailed discussion of “Aristote et l’éthologie” (1993), primarily focused upon *Historia Animalium*, books 8 and 9. Liliane Bodson (1996) concentrated on Aristotelian accounts of bird behavior. Aristotelian zoological writings considered behavior in all kinds of animals known to ancient Greeks, but with more information on birds than on any other group—birds being most easily observed. Bodson focused upon reproductive behavior, from courtship to raising young and found information reported was impressively accurate. An example she discussed in detail was European cuckoo brood parasitism (*HA* 618a:26-31). Jason Tipton’s studies (2006, 2008) focused on habits of rocky near-shore giant goby *Gobius cobitis* and intertidal blenny *Parablennius sanguinolentus*, and upon foraging interactions between mullet (*Mullus* spp) and sea bream (*Diplodus* spp) in Aristotelian writings (Fig. 2).

Animal studies received a boost from the less scientifically sophisticated Roman author, Gaius Plinius Secundus (Pliny the Elder, about 23–79 AD), whose encyclopedic *Naturalis Historia* was a compendium

of Greek and Roman nature writings (Singer 1982:261, Egerton 2001b:245, Egerton 2012:12–13). Although not very successful in his attempt to separate fact from fiction, Pliny exerted a broad influence during the Middle Ages and later in the Latin West, though not in the Byzantine East (Egerton 2002a) or in Muslim civilization; Arabic language nature writings were influenced by Aristotelian works and Byzantine tradition (Singer 1982:262, Egerton 2002b, c, 2012:17–24).

A west European emperor, Friedrich II (1194–1250), lived mainly in Sicily, where he was influenced by Latin, Byzantine, and Muslim civilizations, and he introduced falconry into Western Europe from the Muslim East (Allen 1951:398–400, Stresemann 1951:8–11+2 plates, 1975:9–12, Egerton 2003a, 2012:25–27, Birkhead 2008:137–142). His treatise on falconry included his own observations not only on hawks used for hunting, but also on birds which his hawks pursued. His natural history achievements made him an amateur avian ecologist and behaviorist. His *De arte venandi cum avibus* was published in 1596, but only attracted ornithologists' attention in 1788.

The Latin Middle Ages also produced several encyclopedists, who blended ancient and medieval learning (Singer 1982:263). Some of them were more sophisticated than Pliny, though also accepting some stories now considered incredible. The best of these encyclopedists was German scholastic Albert of Lauingen (Albert the Great, about 1200–80), who studied in Paris about 1240, and then taught there



Fig. 2. School of Athens. Fresco, 1510–11. Raphael. Vatican. Aristotle's Lyceum was a forerunner of European universities, but probably had less grandiose buildings than Raphael imagined. Web.

until 1248, before settling in Cologne to teach (Wallace 1970). His *De animalibus libri XXVI* was his longest and most influential encyclopedia, begun between 1256 and 1260, and drawing upon Aristotelian and medieval sources and his own observations are in books XX–XXI (Allen 1951:400–401, Stresemann 1951:11–12, 1975:12–13, Egerton 2003*b*, 2012:27–30, Birkhead 2008:see index). However, his books XXII–XXVI are based, without acknowledgment, upon *De natura rerum* of his former pupil, Thomas of Cantimpré (1186/1210–76/94), who studied under him in 1245–48 before completing his studies in Paris (Aiken 1947, Kibre 1976). One of the medieval tales which Albert repeated was about the osprey (Albertus 1999:599): “It hunts only fish and has one webbed foot, for swimming, like that of a goose, while the other foot has hooked talons for seizing, like that of an eagle.” A more credible report concerned geese, which bred in Sclavia at “moist, sandy, marshlike places,” but at the beginning of winter they “come back to our land,” seeking “food and the more temperate air” (Albertus 1999:613) (Fig. 3).

Johann Gutenberg’s development of a mechanical printing press in the 1450s gave an enormous impetus to the writing and reading of books in Western Europe. Natural history was an immediate beneficiary, because the printing press stimulated the writing of new natural history encyclopedias (Sarton 1953:52–132, 1957:128–171). An early example was by Englishman William Turner (about 1508–68), physician and father of British ornithology, whose *Avium praecipuarum quarum apud Plinium et Aristotelem mentio* (1544, English 1903) was the first scientific natural history of birds (Raven 1942:48–137, Stresemann 1951:13–15, 1975:13–15, Webster 1976, Bircham 2007:23–33). Although organized around names and observations from Aristotle and Pliny, he added his own observations. One of Turner’s longest and best accounts (Turner 1903:119–121) was on the great gray shrike *Lanius excubitor*:

It has short wings, and flies as if by bounds upwards and downwards. It lives on beetles, butterflyflies, and biggish insects, and not only these, but also birds after the manner of a Hawk. For it kills Reguli and Finches and (as I once saw) Thrushes; and bird-catchers even report that it from time to time slays certain woodland Pies, and can put Crows to flight. It does not seize the birds it kills with its claws, after a swift flight, as Hawks do, but attacks them stealthily and soon (as I have often had experience) aims at the throat and with its beak squeezes and breaks the skull.... when prey happens to be more plentiful, it lays by some for future scarcity. For it impales and hangs the bigger flies and insects on the thorns and spines of shrubs...

An illustration of this shrike is below, Fig. 5b.

A fellow English physician was Edward Wooton (1492–1555), older than Turner, but whose *De Differentiis Animalium* (1552) appeared after Turner’s *Avium* (Bodenheimer 1928–29:I, 230–233, Raven 1947:40–42, Wheeler 1976). It was much broader in scope than *Avium*: chapters 5 on “quadrupeds that bear live young,” 6 on “quadrupeds that lay eggs,” 7 on birds, 8 on fish, 9 on insects, and 10 on squids, crustaceans, mollusks. It was an efficient compilation from previous works, but contained few, if any, first-hand observations.

Some pioneer Renaissance naturalists added illustrations to their books. German physician Otto Brunfels (about 1489–1534) compiled *Herbarum vivae eicones* (three volumes, 1530–36, German, two volumes, 1532–37) with traditional text, but with fresh woodcuts by artist Hans Weiditz (Stannard 1970,

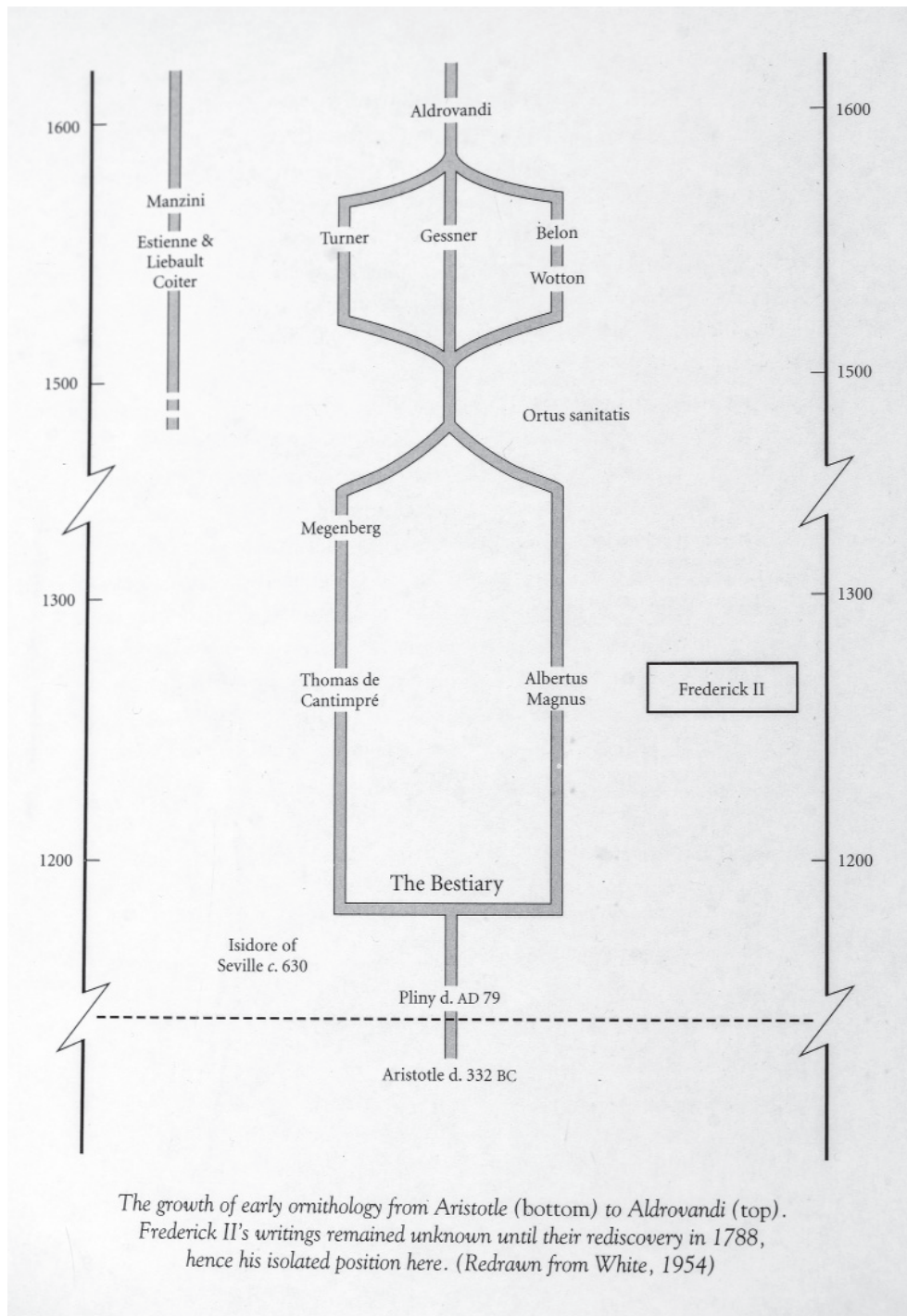


Fig. 3. Growth of ornithology from Aristotle to Aldrovandi. T. H. White. Redrawn in Birkhead 2008:20.

Reeds 1976, 1991, Greene 1983:1, chapter 5). Once Weiditz got started, he kept going until he had illustrated 47 plants not represented in classical pharmacopoeia. Brunfels apologized for including them, but added names and descriptions of them.

Conrad Gessner (or Gesner, 1516–65) of Zurich, compiled a well-illustrated *Historia animalium* (5 volumes, 1551–87, German edition, 4 volumes, 1557–89) and a posthumously published *Historia plantarum* (1751–71), both of which included his own observations along with traditional learning (Allen 1951:402–403, Stresemann 1951:18–22, 1975:18–21, Greene 1983:II, 747–797, Wellisch 1984, Egerton 2003:206–208, 2012:34–40). Gessner supported his family by being both a professor at the University of Zurich and as a physician, and when an epidemic of plague reached Zurich, he died along with the patients he treated. Englishman Edward Topsell (1572–1625) published a translation of Gessner's first volume on mammals and extracts from Gessner's volumes 2, 4, and 5 as his own second volume in 1607 (Raven 1947:217–226, Bircham 2007:71–73, Birkhead 2008:36–37).

An Italian naturalist-encyclopedist, Ulisse Aldrovandi (1522–1605), continued in Gessner's footsteps (Bodenheimer 1928–29:I, 247–276, Allen 1951:403–405, Stresemann 1951:22–24, 1975:see index, Castellani 1970, Beier 1973:85–86, Singer 1982:263, Aguilar 2006:29–30), even to the point of using Gessner's work with scant acknowledgment. He did not manage to publish all of his works before he died, though he did publish three volumes on birds (1599–1603) and one on insects. Studies on insects arose in antiquity and continued on through the Middle Ages and Renaissance (Bodenheimer 1928–29:I, 11–240, Beier 1973:81–84, Morge 1973, Aguilar 2006:15–20), and entomology emerged as a separate science with Aldrovandi's publication of *De Animalibus Insectis libri VII* (1602, edition 3, 1628). In other volumes he drew heavily upon Gessner's volumes, however, Gessner died before finishing his insect volume, and so Aldrovandi depended more on his own observations for this volume. Raven (1947:191) was unimpressed with the results.

Gessner was not the only naturalist from the 1500s who died before completing his volume on insects. English physician-naturalist Thomas Penny (about 1530–89) spent most of his career studying British plants (Boulger 1896, Raven 1947:153–171, Desmond 1977:488). However, he had traveled in Europe after his medical education, had been with Gessner while he was working on insects, and possibly brought back to England Gessner's notes and illustrations on insects. When he turned to the study of insects himself in his later years, he had Gessner's materials to aid his own endeavors, and when he died, those insect materials were acquired by a friend, Thomas Moffett (Moufet, Muffet, 1555–1604), another English physician-naturalist, who focused upon insects (Bodenheimer 1928–29:I, 276–289, Beier 1973:86, Simpkins 1974, Aguilar 2006:28). Moffett prepared the manuscript for publication, but failed to find a publisher. After Moffett died, the manuscript was bought by Sir Theodore Mayerne, who finally got it published in Latin in 1634 under Moffett's name (English, 1658, 1967).

The Aldrovandi and Penny-Moffett volumes were written independently at about the same time, though the latter was delayed three decades before publication. Bodenheimer and Beier (cited above) evaluated them. Both volumes had strengths and weaknesses, and together they stimulated several other insect compendia during the 1600s. The Penny-Moffett volume has the advantage of now being in English, recently reprinted. In it, there is an adequate illustration and verbal description of a praying mantis, but the natural history contains this nonsense: "So divine a creature is this esteemed, that if a childe aske the way to such a place, she will stretch out one of her feet, and shew him the right way, and seldome or never misse" (Moffett 1658:983) (Fig. 4).

English clergyman-naturalist John Ray (1623–1705) followed the encyclopedic tradition in his *Catalogus plantarum circa Cantabrigiamnascentium* (1660), *Historia plantarum* (three volumes, 1686–1704), and *Historia insectorum* (1710), but he went beyond that tradition in other works. He published under

the name of his former student and deceased patron, Francis Willughby (1635–72), *Ornithologia* (1676, English 1678), which modern scholars conclude was actually more than half by Ray (Raven 1942:308–336, Keynes 1961:52–55, Bircham 2007:59–71, Birkhead 2008:see index), and the same was true of their *De Historia Piscium* (1686) (Raven 1942:339–369, Keynes 1961:65–72). Ray had an early interest in insects and discussed their habits in some early publications, but only in his old age did he write two treatises on them: *Methodus Insectorum* (1705) and *Historia Insectorum* (1710), both appearing posthumously (Raven 1942:388–418, Keynes 1961:134–138, Mickel 1973). Concurrently, he also published theoretical works (Zeit 1994, Mandelbrote 2004): *The Wisdom of God Manifested in the Works of the Creation* (1691) and *Miscellaneous Discourses concerning the Dissolution and Changes of the World* (1692).

In her monograph, “The Role of Territory in Bird Life,” Margaret Morse Nice quoted Ray’s *Ornithology* (1678:222) on the nightingale (1941:441):

It is proper in this Bird at his first coming (saith [G. P.] Olina [1622]) to occupy or seize upon one place as its Freehold, into which it will not admit any other Nightingale but its mate.

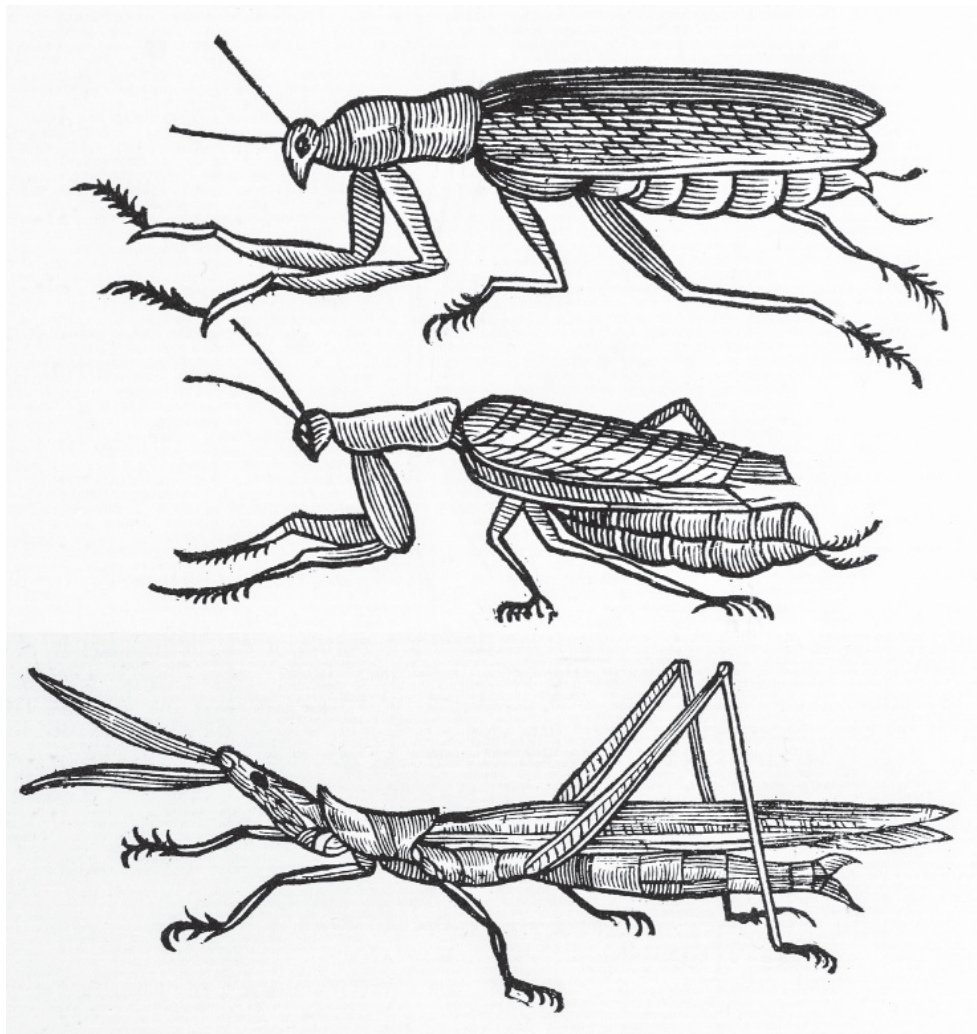


Fig. 4. Praying mantis. Moffett 1658:983.

However, Ray omitted part of Olin's statement, added by Nice: "it ordinarily sings in its freehold."

Ray exerted a strong positive influence upon British and North American natural history studies (Thorpe 1979:4–8, Egerton 2005, 2012:60–64). His disciple, Rev. William Derham (1657–1735), wrote a comparable natural history treatise, *Physico-Theology, or a Demonstration of the Being and Attributes of God*, from his *Works of Creation* (1713, edition 4, 1716), also widely read (Knight 1971).

Dutch small businessman Antoni van Leeuwenhoek (1632–1723) discovered the microscopic world by grinding his own lenses and examining canal water and other ordinary substances (Schierbeek 1959, Egerton 1968, 2006a, 2012:64–66, Heniger 1973). His discoveries were considered important enough for him to be elected a member of the Royal Society of London, and his reports were regularly published in English translation in that society's *Transactions*. He observed hydra and rotifers eating objects smaller than they, and he even discovered bacteria, from his own mouth. He also studied other small life, such as the insects found in galls on oak leaves. He found that trees lay down annual rings as they grow, and that eels do the same in their scales. He did not suggest that his "little animals" might cause disease, but others did.

Austrian nobleman Johann Ferdinand Adam Pernau (1660–1731) was in a Protestant family that immigrated to Franconia, Germany. He earned a doctorate degree at the University of Altdorf (Stresemann 1925, 1947, 1951:289–291, 1975:287–289, Singer 1982:265, Birkhead 2008: see index). After marriage he acquired a rural estate where he studied nature, primarily birds. In 1702, he published anonymously a small book of his observations (94 + 12 pages), which he twice enlarged (1707, 240 + 62 pages, 1716, 318 + 49 pages). His fellow nobles were only interested in shooting wildlife, and he wanted to show that study of living animals could be rewarding. He studied wild birds both in the field and in captivity, and he experimented by sending "a bird away for several miles (as I have frequently done) and to see it returning to its owner" (Pernau 1716:201, translated by Stresemann 1947:40). He concluded that partridges stick together during winter because singly they could not effectively scratch through snow to food, but together they could. Other birds had different needs:

...the Nightingale is forced, for the sake of her feeding requirements, to chase away her own equals, for if many would stay together, they could not possibly find enough worms and would inevitably starve (Pernau 1716:242–243, translated by Stresemann 1947:43).

Pernau "finds his equals in only a few ornithologists of our day, and may be ranked with Oskar Heinroth and Konrad Lorenz" (Stresemann 1947:39) (Fig. 5).

René Antoine Ferchault de Réaumur (1683–1757) was a prominent, versatile French scientist who devoted most of his attention to insects (Tuxen 1973:97–99, Gough 1975, Egerton 2006b, 2012:74–77). His *Mémoires pour servir à l'histoire des insectes* (6 volumes, 1734–42) was a monumental achievement (Bodenheimer 1928–29:I, 415–448, II, 379–399). He was not attracted by the goal of describing and classifying all the species he could find. Rather, he studied behavior of common species. He wrote two memoirs for a volume 7, which he never finished or published, but they appeared about two centuries later (de Réaumur 1926, English, 1926, 1977, de Réaumur 1955). His "Histoire des Fourmis" was "the most important myrmecological document of the eighteenth century," and Réaumur was also "the founder of ethology" (Wheeler 1926:xvi, 36).

de Réaumur was also one of the first experimenters on animal behavior. His simplest experiment was to transfer most of an ant colony to the confines of a glass bell jar so that he could observe their activ-

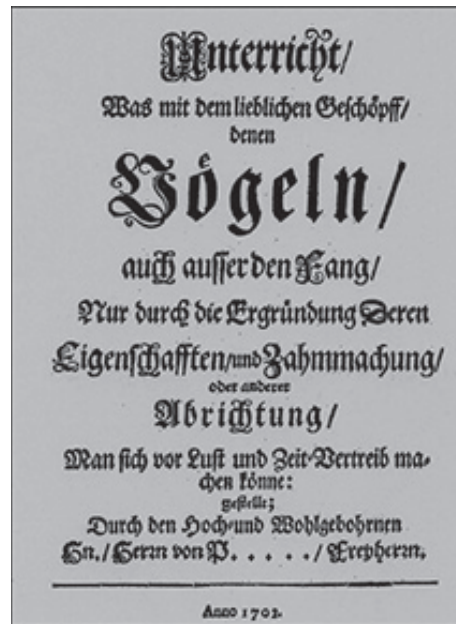


Fig. 5. Pernau's title page of his 1702 book, anonymous, Unterricht, Was mit dem lieblichen Geschopff, denen Vogel[n]....

ities (1926:French, 54–55; English, 142–143). He also added food to keep them alive and functioning somewhat normally. He did not persist long enough to answer all the questions which he raised, such as whether ant colonies (de Réaumur 1926:French, 88–89; English, 177):

...are founded like those of the wasps, by a single mother, without the aid of any worker, or whether they are founded by one or several females that are accompanied by several workers for the purpose of taking charge of operations.

The answer was not one or the other alternative; Wheeler (1926:247, note 71) said both types of colony formation occur among different ant species. Réaumur's influence upon other naturalists of the 1700s and early 1800s was extensive.

As de Réaumur's career was winding down in the 1740s, the career of a countryman and, briefly, a rival, Georges-Louis Leclerc, Comte de Buffon (1707–88) was taking off (Buffon 1954, Roger 1970, 1997, Egerton 2007a, 2012:84–86). Buffon obtained the directorship of the Jardin des Plantes in Paris, a very prestigious position that enabled him to publish, with royal sponsorship, an elaborate multi-volume *Histoire naturelle, générale et particulière* (44 volumes, 1749–1804). It included 12 volumes on mammals (1753–67) and nine volumes on birds (1770–83), both sets well-illustrated. These 21 volumes gave broader and more detailed coverage of mammals and birds than ever before. Unfortunately, his ready access to animals and literature convinced him that he could draw broad generalizations based upon what we now see was inadequate data.

An example of his over-confidence is his discussion of deer. He did not bother using Linnaeus' scientific names, believing that common names, along with illustrations was sufficient. His account of Europe's red deer began with a discussion of hunting it, and then discussed its natural history throughout the seasons. He

stated (1780:IV, 99): “Vegetation may...be reduced to three kinds. The first, in which the growth proceeds from the superior extremely, as in plants, trees, and the wood of the stag...” Elsewhere (vol. 9, 1761), in a discussion “Of Animals peculiar to the New World,” he stated (1780:V, 115): “If we reckon that 200 species of quadrupeds [mammals] exist in the whole known quarters of the globe, we shall find above 130 of them in the Old Continent, and less than 70 in the New; and, if we subtract the species common to both Continents... the New World cannot claim above 40 native species. In America, therefore, animated Nature is weaker, less active, and more circumscribed...animals are much smaller than those of the Old Continent.”

By 1783, Thomas Jefferson (1743–1826) was a U.S. Ambassador in Paris, negotiating a peace treaty with Britain, following the War of Independence. He was also in the midst of writing his Notes on the State of Virginia (French, 1785, English, 1787), and he took umbrage at Buffon’s claim that American mammals were inferior to those of the Old World, and he responded by writing an extensive refutation, with tables of data, in his Notes (1984:169–185), and he obtained from America the bones and skeleton of a moose—larger than any deer in Europe—to present to Buffon (Dugatkin 2009a) (Fig. 6).

A French “lieutenant des chasses des Parcs de Versailles, Marly et dépendances,” Charles-Georges Le Roy (1723–89), inherited his office in the royal service from his father (Anderson 1994:1). What raised Le Roy above the level of a royal game keeper was his relationships with encyclopedists Diderot, d’Alembert, and Helvétius, for whom he wrote articles, including one on instinct. Both Gray (1968:377–379) and Thorpe (1979:10–13) judged Le Roy to have been the most important early contributor to the study of animal behavior. His achievement was in his *Lettres sur les animaux* (1994, 1768, English, 1870). Gray and Thorpe mistakenly give its date as 1764, whereas only a few of his letters had been published separately by then (Anderson 1994:14–15).

Le Roy urged anyone who wants to understand animals to (1870:10):

Leave his study, and plunge into the woods, there to follow every wile and turn of these sentient beings, to appreciate the development and effects of this faculty of feeling, and to see how by repeated sensations, combined by memory, they rise from mere instinct to intelligence.



Fig. 6. (a) Réne-Antoine Ferchault de Réaumur. Web. (b) Charles-Georges Le Roy. Wikipedia.

Le Roy stated that Steller and Buffon had provided examples, and that he would “like to have the complete biography of every animal” (1870:11). He was envisioning such a science as ethology would become, and he provided the insights in his books that an alert game keeper could observe (Birkhead 2008:110–112).

German Protestant Pastor Ernst Spitzner (1788) described the dance of honeybees (quoted in Lindauer 1985:129):

Full of joy they twirl in circles about those in the hive, from above downward and from below upward. In a few minutes, after these had made it known to the others, they came in great numbers to the place!

This anticipation of von Frisch (1920-22) apparently had no influence on later behavioral studies.

English clergyman-naturalist Gilbert White (1720–93) studied in detail the natural history of his village, Selborne, and its surroundings (Fitter 1959:12–38, Mabey 1986, Dadswell 2003, Foster 2004, Burkhardt 2005:71–72, Egerton 2007a,b, 2012:89–92). Natural history was not an academic course in universities. One learned it mainly from natural history literature, and for him, especially from the writings of Ray and Derham. White’s *Natural History and Antiquities of Selborne* (1789), due to his persistent observations and engaging writing style, has stayed in print down to the present, though modern editions, such as Anne Secord’s (2013), usually omit the *Antiquities*. She added illustrations of birds and mammals to her edition from Thomas Pennant’s *British Zoology* (1768–70), which is quite appropriate since 44 of the letters (instead of chapters) in White’s *Natural History* were addressed to Pennant (1726–98), and Pennant incorporated some of White’s observations in his own treatise (Urness 1974). James Harting illustrated his edition of White’s *Selborne* (1887) with woodcuts by Thomas Bewick, a later contemporary of White’s. White began his letters to Pennant in 1767, and he began keeping journals in 1768, and continued doing so until he died. His journals were filled with what we call phenological observations, with several entries for each week (White 1971). He could then supplement his letters on specific subjects with background information from his journals. White’s natural history consisted primarily of his own observations on the mating, eating, and raising young of the wildlife he observed, with speculations about migrations vs. hibernation of swallows, and also on the life cycles of plants observed. He read other natural history writings and sometimes confirmed or challenged what others wrote on topics he studied (Fig. 7).

White distinguished among three very similar species of willow wrens (= leaf warblers *Phylloscopus*) on the basis of their different songs (letters to Pennant 16 [18 April 68] and 19 [17 August 68]), but Gray (1968:373) commented that White had failed to generalize from this discovery, that song and other behaviors can be important means to distinguish similar species. But White wrote at a time when the only significant generalization in natural history was the balance of nature (Egerton 1973). One generalization White did make concerned territory, in his letter 11 to Daines Barrington (8 February 1772):

...during the amorous season, such a jealousy prevails between the male birds that they can hardly bear to be together in the same hedge or field. Most of the singing and elation of spirits of that time seem to me to be the effect of rivalry and emulation and it is to this spirit of jealousy that I chiefly attribute the equal dispersion of birds in the spring over the face of the earth.



Fig. 7. White's home at Selborne, The Wakes, from the back. Wikipedia on White.

White did not trumpet this insight as a key factor in bird behavior, nor did he take it as a hypothesis to be verified. Still, Cambridge University author Peter Bircham called White “the father of British ornithological ecology” (2007:100).

Englishman Oliver Goldsmith (1728–74), poet, playwright, and popularizer of natural history, is the first known user of the term territory in its modern context Goldsmith (1774:V, 301, cited from Nice 1941:443):

...small birds mark out a territory to themselves, which they will permit none of their own species to remain in: they guard their dominions with the most watchful resentment: and we seldom find two male tenants in the same hedge together

Goldsmith published this after White wrote his letter to Barrington, but before White published that letter.

English physician, Erasmus Darwin (1731–1802), wrote on evolution (McNeill 2004, Fara 2012:see index), and although his contemporaries seem not to have been much influenced by what he wrote, his grandson, Charles Darwin, was respectful of his grandfather (who had died before he was born), read his books, and even wrote his biography (Darwin 2003). Erasmus Darwin's *Zoonomia* (1794:chapter 39: “Of Generation”) contained his ideas on evolution being influenced by desires and striving (Darwin 1968:85):

...animals undergo perpetual transformations; which are in part produced by their own exertions in consequence of their desires and aversions, of their pleasures and their pains, or of irritations, or of associations; and many of these acquired forms or propensities are transmitted to their posterity.

...three great objects of desire, which have changed the forms of many animals by their exertions to gratify them, are those of lust, hunger, and security.

Thomas Bewick (1753–1828) was an exceptional engraver of animal illustrations who wrote natural history books on world mammals (1790) and British birds (1797), both books going through numerous editions (Bewick 1981, Bircham 2007:159–163, Uglow 2007). He elevated woodcuts from being a useful device for printing illustrations into an art form, though still used

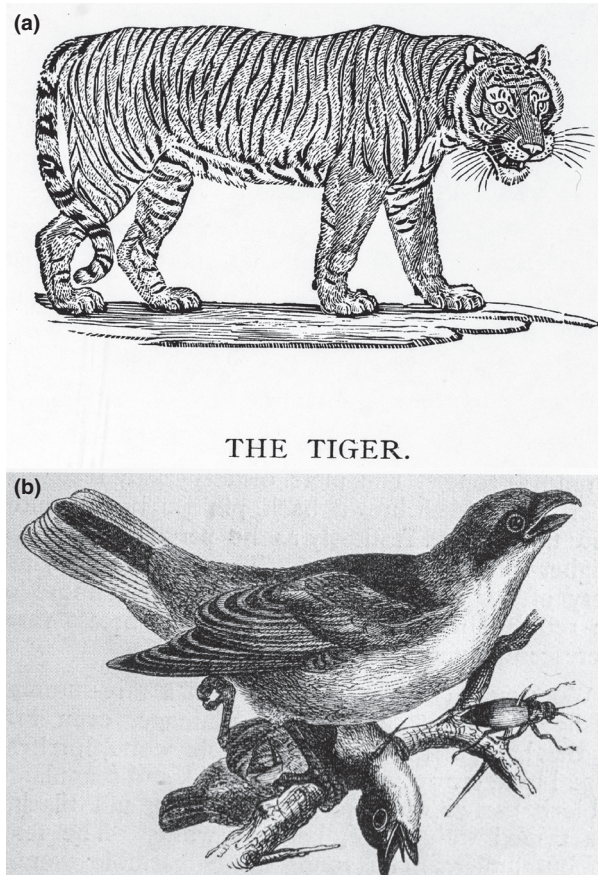


Fig. 8. (a) Tiger. Bewick 1811:206. (b) Great gray shrike. Bewick 1797. From Bircham 2007:31.

for book illustrations (Bell 2015, Donald and Donald 2015). Although he studied first hand some British mammals and birds, natural history works by his time were so readily available—such as Buffon’s on mammals (translated into English in 1780) and on birds (translated in 1792–93) (Wood 1931:267–269)—that he undoubtedly obtained much of his information from such works (Fig. 8).

Frenchman Jean Baptiste de Lamarck (1744–1829) is most remembered for his theory of evolution (transformism) due to use or disuse of organs, and inheritance of acquired traits (Burlingame 1973, Burkhardt 1977, Thorpe 1979:13–14, Singer 1982:266). The shift in Lamarck’s belief from unchanging to changing species occurred during the French Revolution, which he supported, and opposition to the concept of evolution came from his nemesis, Georges Cuvier (1769–1832), who also opposed the Revolution (Egerton 2010a:21, 2012:131–132). The theoretical climax of Lamarck’s case for evolution was in his *Philosophie Zoologique* (1809, English 1914, 1984), which did discuss animal behavior. His system of invertebrate (*sans vertebrae*) classification was based upon the degree of development of their nervous system (Singer 1982:266). Cuvier’s outlook dominated France, but his colleague, Étienne Geoffroy-Saint-Hilaire (1772–1844) defended Lamarck’s ideas on transformism (Bourdier 1972a, Thorpe 1979:14–15). In 1825, Geoffroy argued that a crocodile-like fossil, which he named *Teleosaurus*, was an intermediate between reptiles and mammals (Bourdier 1972a:357).

English author William Bingley (1774–1823) earned a B.A. from Cambridge University (1799) and became a Fellow of the Linnean Society (Courtney 1885). His career resembled Pennant's in that Bingley published a book of travels through north Wales (1800), followed by two natural history works, *Animal Biography* (1802, edition 7, 4 volumes, 1829) and *Memoirs of British Quadrupeds* (1809). Only his travel book would likely have contained much original observations, but the other two indicate the popularity of natural histories among the British (and American) public, despite being “highly credulous writings” (Thorpe 1979:25).

Scots immigrant to the United States Alexander Wilson (1766–1813) settled in Philadelphia, where he was influenced by native naturalist William Bartram (Allen 1951:552–569, Hunter 1983, Egerton 2009:454–459, 2012:127–128, Burt and Davis 2013). He decided to describe and illustrate all the birds of America, which at the time, meant east of the Mississippi River. He emphasized their habits from his own observations and from relevant literature. His *American Ornithology* (9 volumes, 1808–14) was conceived on a grand scale, with his illustrations of birds hand-colored, and nine of an anticipated ten volumes appeared, the last two after his early death. His friend, George Ord, wrote volume nine from Wilson's notes. *American Ornithology* was a monumental achievement, which earned Wilson the title of Founder of American Ornithology. His opus went through about nine or ten editions by 1878, some of which included supplementary studies by Charles Lucien Bonaparte, and later editions with black-and-white plates (Wood 1931:630–631).

The most popular subjects for animal behavior studies were vertebrates, but insects ran a close second. The very popular illustrated *Introduction to Entomology* (4 volumes, 1815–26) by William Kirby (1759–1850) and William Spence (1783–1859) has been discussed previously (Egerton 2012:185–186, 2013:36–38), and here the focus is on their natural history studies. Five of their chapters describe injuries which insects cause to humans and crops, two chapters are on insect benefits, and 18 chapters are on various aspects of behavior. Their latter discussions include: care of young, food, habits, societies, defense, locomotion, sounds, illumination, hibernation, and instincts.

French immigrant Jean Jacques Audubon (1785–1851), who anglicized his first two names after coming to America, was more flamboyant than the serious Wilson, and he aspired to outdo Wilson with his own illustrations for *Birds of America* (4 volumes, 1827–38), and in some respects he did, often conveying action in his illustrations for *The Birds of America* (4 volumes, 1827–38, with 155 plates; Herrick 1917, Ford 1964, Streshinsky 1998, Rhodes 2004, Souder 2004, Vedder 2006). However, Audubon was not as cautious as Wilson concerning scientific information in his *Ornithological Biography* (5 volumes, 1831–39). Audubon came up short in his attempt to paint all the birds that Wilson had, and therefore he copied five of Wilson's figures without acknowledgment (Welker 1955:48–58+ figures 7–12, Hunter 1983:93–97+ figures 15A–17B). A good number of editions of *The Birds of America* have appeared until very recent times, some of which Wood (1931:207–209) cited.

Audubon in April 1804 tied silver threads on the legs of young pewees along the banks of the Perkioming Creek above its joining the Schuylkill River, at his father's Mill Grove farm on a road to Philadelphia. He wanted to know if any of them would return to the same region in 1805, when he found two of them near the site where they were banded (Audubon 1831–39:II, Herrick 1917:II, 107–108, Rhodes 2004:37). This seems to be the first time birds had been banded in order to study aspects of their natural history, which achieved results. Audubon also conducted experiments on whether vultures can smell (Audubon 1826–27), and concluded that two American species could not.

An unsuccessful banding effort also occurred in 1804 (Lincoln 1933:65–66): Brugmann, a Dutch naturalist, marked some White Storks (*Ciconia alba*), in an effort to ascertain whether they would return to the place of their birth. The method of marking is not known, but the experiment did not produce any usable information (Fig. 9).

Like Wilson, Audubon traveled widely to study birds, and in Charleston, South Carolina, he met in 1831 amateur naturalist Rev. John Bachman (1790–1874), who had become interested in birds during an earlier acquaintance with Alexander Wilson (Shuler 1995, Stephens 1999, 2000). Audubon and Bachman liked each other, and Bachman provided information for Audubon on local birds. Eventually, Audubon’s two sons married Bachman’s two daughters. As Audubon was finishing work on American birds, he and Bachman began collaborating on a comparable work on American mammals, in which Audubon’s sons also helped. In 1842, Audubon began planning a last expedition, up the Missouri in quest of mammals, which began in March 1843 and returned home in November (Rhodes 2004:417–430). Audubon painted over half of the plates and his son John W. Audubon painted the rest. His other son, Victor, handled publication of the *Quadrupeds* (30 parts with five plates each, collected as three volumes, 1845–53). Unfortunately, two editions that appeared in 1951 and 1989 omitted Bachman’s name from their title pages.

In 1823, a German, N. Unhoch, published “an almost perfect description of the rounddance” of bees (quoted in Lindauer 1985:129):

The dance mistresses twist and turn in something more than a semicircle, now to the right, then to the left, five or six times, and execute what is a genuine round dance.

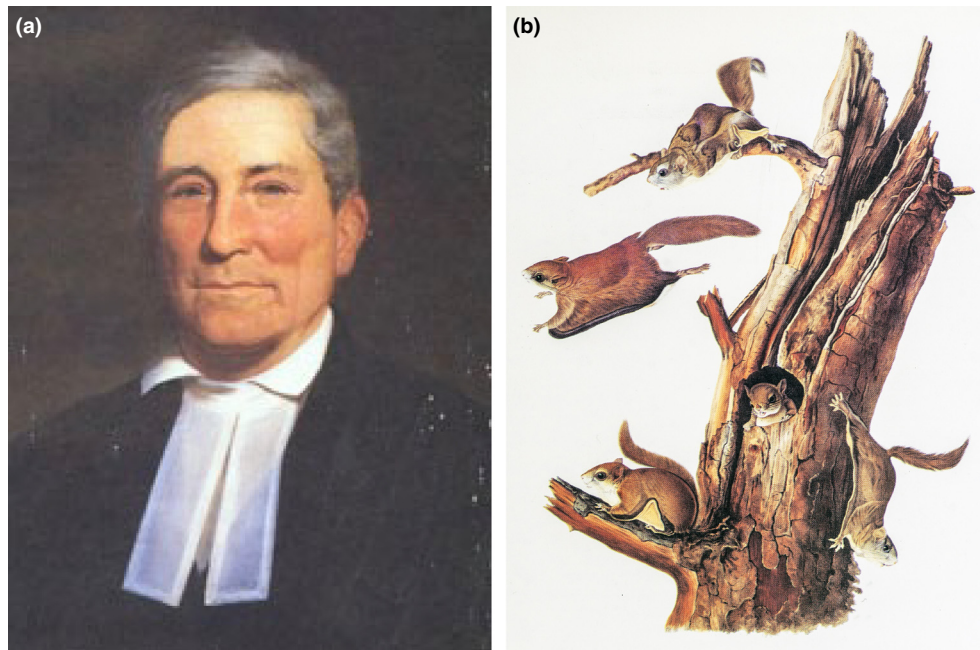


Fig. 9. (a) John Bachman. By John W. Audubon. About 1837. Now at Charleston Museum. Web. (b) Eastern Flying Squirrel. Plate 28 (figs. 1,2, males, 3,4, females, 5, young). Audubon 1979:595 or Audubon [and Bachman] 1989:99.

But Unhoch lacked understanding of its function. In retrospect, what three previous amateur observers of honeybee dancing lacked which Frisch had, was excellent zoological training and persistence.

In summer 1832, Audubon traveled to Boston and met an English botanist, Thomas Nuttall (1786–1859), who was then curator of the Harvard University Botanic Garden and also lecturer on natural history at Harvard (Beidleman 1960, Graustein 1967:242–253, Thomas 1974, Savage 1979:174–188). They “clicked” immediately, for Nuttall had been an explorer of the West before Audubon, and he was interested in birds as well as plants. They shared information on birds, on which both were preparing comprehensive works. Wilson and Audubon were ornithological explorers, who published their findings in multi-volume works as they discovered them, but Nuttall systematically organized his *Manual of the Ornithology of the United States and of Canada* into two volumes: *The Land Birds* (1832, viii + 603 pages) and *The Water Birds* (1834, vii + 627 pages), both volumes with uncolored illustrations. He integrated his own life history observations with those of Wilson, Audubon, and others. Nuttall’s *Manual* received positive reviews, and new editions appeared in 1840, 1891, 1894, and 1903 (Wood 1931:496). Nuttall’s biographer, Jeannette Graustein, provides maps of his six western journeys Graustein (1967:46–47, 134–135).

George Thomas Bettany (1789–1870) was a physician in his native fishing village, Polperro, on the Cornwall coast (Bettany 1887). In his early adult life he had assisted Bewick. He became Polperro’s leading citizen. His greatest natural history achievement was his *Fishes of the British Islands* (4 volumes, 1860–65), which included his own colored illustrations, many of which were drawn from fish supplied by Polperro fishermen. He published articles in the *Linnean Society Transactions*, *Magazine of Natural History*, and *Annals of Natural History*. Of interest here is his *Illustrations of Instinct, Deduced from the Habits of British Animals* (1847, 343 pages), which Thorpe (1979:25) considered credulous writing. Couch died leaving 12 volumes of unpublished natural history notes, still preserved. His *Cornish Birds* was based upon notes begun in 1829, and published in 2003 (Fig. 10).

Charles Darwin (1809–82) transcended the natural history tradition with his revolutionary theory of evolution by natural selection, but he nevertheless also contributed to the natural history literature. His *Journal of Researches into the Geology and Natural History of the Voyage of H. M. S. Beagle* (1839) was an excellent example of natural history exploration literature (Browne 1995, Egerton 2010b, 2012:143–146). On the *Origin of Species* (Darwin 1859:207–244) contained a chapter on instinct. However, he declined to define it (1859:207):

I will not attempt any definition of instinct. It would be easy to show that several distinct mental actions are commonly embraced by this term; but every one understands what is meant, when it is said that instinct impels the cuckoo to migrate and to lay her eggs in other birds’ nests.

He devoted the chapter mostly to social insects, because he recognized a challenge to his theory of natural selection in the existence of non-reproducing worker bees (Richards 1987:142–152, Prete 1990, Borrello 2010:7–14). To celebrate the centenary of *On the Origin of Species*, British biologists published two collections of studies on Darwin’s work, which included two commentaries on his behavioral studies (Barnett 1958, Maynard Smith 1958), and one on studies on animal communication since Darwin (Marler 1959).

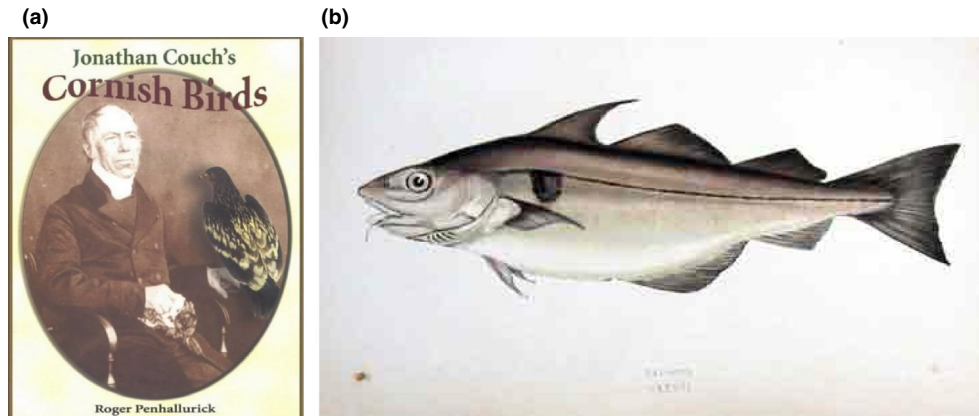


Fig. 10. (a) Jonathan Couch: title page of his *Cornish Birds* (2003). (b) Couch drawing of fish. Both at web site.

The *Origin* was the pinnacle of Darwin's achievements, but by no means the end of his researches (Boakes 1984:1–8, Richards 1987, Browne 2003, Egerton 2011, 2012:165–168). His next book was *On the Various Contrivances by which British and Foreign Orchids are Fertilized by Insects* (1862). If his main general message was a struggle for existence, it was not conspicuous in this book, devoted to co-evolution between orchids and insects to their mutual benefit, and on the forms various orchid species have evolved in order to guide insects in their collection of nectar in such a way as to ensure cross-pollination of orchid flowers. One could argue that Darwin was the effective founder of ethology in three works: the *Origin* (1859), *The Descent of Man*, and *Selection in Relation to Man* (1871), and *The Expression of the Emotions in Man and Animals* (1872), though without using the term ethology (Thorpe 1979:see index, Burkhardt 1985, Richards 1987:185–242, Dugatkin 2006:1–10). Some drawings in *Expression of Emotions* were by T. W. Wood. Thorpe (1979:24) thought the book “had a tremendous influence on the development of the study of animal behaviour, in that here was an outstandingly original comparative study of behavior, a true pioneering achievement.” Despite its qualities, however, the book did not have much immediate impact, which Thorpe attributed to the fact that Darwin's revolution was so broad that biologists could not get to all aspects of it simultaneously (Fig. 11).

New York State lawyer Lewis Henry Morgan (1818–81) was heavily involved in politics and business, but also in scholarly research (Hodge 1934, Gray 1967, 1968:381–383), and has been called “Father of American Anthropology.” He also wrote *The American Beaver and His Works* (1868), after beaver had been trapped out of most of its former range, prior to European settlement. Beavers' role in the historic fur trade was well known, but its natural history was not. Chapter one Morgan entitled “Characteristics and Habitat,” and chapter nine, “Animal Psychology.” He was unable to give any definitive answers on this complex subject, but his discussion might challenge others to explore questions he considered. Also, “Morgan defended the rights of animals with vigor, as he had defended the rights of the Indians” (Gray 1968:383).

Canadian immigrant to England George Romanes (1848–94) became a disciple of Darwin's, during Darwin's later years (Klopfer and Hailman 1967:7–14, Lesch 1975, Thorpe 1979:24–25, Singer 1982:267, Boakes 1984:24–32, Richards 1987:332–342). He published two books to which Darwin contributed: *Animal Intelligence* (1882) and *Mental Evolution in Animals, with a Posthumous Essay on Instinct* by Charles Darwin (1883). *Animal Intelligence* was “the first general treatise on ‘comparative

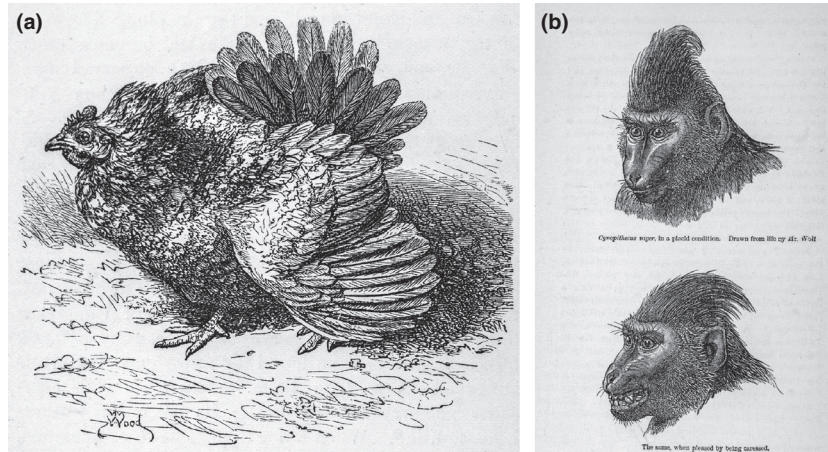


Fig. 11. (a) Hen driving away dog from her chicks. Drawing by T. W. Wood.
 (b) *Cynopithecus niger*, Drawing by Mr. Wolf. Darwin 1888:98, 136.

psychology” (Thorpe 1979:25), but it was somewhat similar to the credulous works by Bingley and by Couch. Yet, Houck and Drickamer thought his *Animal Intelligence* was important enough to include a brief extract in their source book (1996:38–44).

How did Darwin’s contributions differ from those of White? White asked nature how it worked, and he reported what he observed. Darwin’s *Journal of Researches* was within that tradition, but beginning with *On the Origin of Species*, he defended a particular theory on how nature worked, and all his contributions to what we call ethology were contributions to evidence for that theory (Fig. 12).

Londoner Donald Alexander Spalding (about 1840–about 1877), from the working class, attended college for a year and was then admitted to the bar (Gray 1962, 1967, Thorpe 1979:18–26, Singer 1982:267, Boakes 1984:see index). While working in Aberdeen, he attended psychology lectures by Professor Alexander Baines at the University of Aberdeen. He experimented on chicks, before and after hatching, to reveal their instincts and began publishing on instinct in 1872 (Spalding 1873, Gray 1962, 1967). “He felt that instinct and learning go hand in hand in the same species and in the same individual and that the function of instinct is to guide the course of learning, not substitute for learning” (Gray 1967:176). Gray also traced his influence upon later students.

(Jean) Henri Fabre (1823–1915) was from a rural village in southern France and was educated to become a school teacher by 1842 (Peattie 1936:326–347, Fitter 1959:125–142, Klopfer and Hailman 1967:23–24, Théodoridès 1971). He was not satisfied with his situation, however, and continued his studies until he earned a doctorate in science at Paris in 1854. Thereafter, he devoted his time to studying insects and publishing books on his findings, and was cited in Darwin’s *Origin of Species* (1859:218):

*...M. Fabre has lately shown good reason for believing that although the *Tachytes nigra* generally makes its own burrow and stores it with paralysed prey for its own larvae to feed on, yet that when this insect finds a burrow already made and stored by another sphex, it takes advantage of the prize, and becomes for the occasion parasitic.*



Fig. 12. (a) Georges Romanes. Web (color). (b) Jean Henri Fabre. Web.

Fabre was no doubt pleased with Darwin's notice of his work, but he did not accept Darwin's or any other theory of evolution. Fabre's major publication was a series of *Souvenirs Entomologiques* (10 volumes, 1879–1908), containing fifty years of his observations. They were accessible to lay readers, and most were translated into English. In 1949, an American amateur naturalist thought it still worthwhile to republish an anthology of those writings.

Jean Théodoridès, French historian of zoology, commented (1971:508):

Fabre remains the very model of the self-taught scientist—solitary, poor, proud, and independent. He was also an attentive and minute observer and a writer of unquestionable talent.

Solitary naturalists who publish in the popular press might evade pre-publication peer review, but then face post-publication commentary. How did America's foremost entomologist respond to Fabre's death? William Wheeler, no snob, commented (1916:74):

...the world has lost its greatest entomologist, a man who combined in an extraordinary degree the gifts of a virile and penetrating observer and those of a literary artist of high distinction.

Yet, Wheeler knew that French entomologists had not embraced Fabre, and he acknowledged that Fabre was “a crotchety and opinionated recluse” (1916:77). One of those French entomologists, Charles Ferton “point[ed] out the gaps in Fabre's work and complet[ed] his observations” (Richard 1973:485). Ferton's criticism “gave rise to the mechanicalist reaction in France, which was at first fruitful.” Richard cited Ferton's *La Vie des Abeilles des Guêpes* (1923) as an example of his work, which perhaps also discussed Fabre's work.

A German from Munster, Bernard Altum (1824–1900), developed a strong life-long interest in birds as a youth (Stresemann 1975:328–330). Although he became a priest, he moved to Berlin, 1853–57, in order to study zoology and earn a doctorate in philology. After returning to Munster, he taught natural history and ornithology at the Royal Academy, and he published *Der Vogel und sein Leben* (1868). In 1869, Altum became professor of zoology at the Forestry Academy in Eberswalde, and in 1891 he was elected president of the *Deutsche Ornithologische Gesellschaft*. Yet, he also became a determined opponent of Darwin's theory of evolution.

Instead, he claimed: “All individual beings are harmoniously interrelated and thus form a total unified reflection of Nature” (translated in Stresemann 1975:330). He argued that parent birds do not feed their young because of love, but due to a “compulsion to feed birds that have a certain appearance, a certain cry, and a certain way of fluttering their wings and opening their beaks” (in Stresemann 1975:331). He also observed that pairs of birds occupy a territory whose size probably depended upon the amount of food needed to raise their young. He also viewed bird song as used both for attracting a mate and as a notice to other males of the size of their territories.

Two American entomologists not previously discussed by me were New York Stater William H. Edwards (1822–1909) and Bostonian Samuel H. Scudder (1837–1911), both of whom William Leach (2013:see index) discussed as lepidopterists, while Arnold Mallis (1971:185–191, 288–292) listed Edwards as a lepidopterist and Scudder as an orthopterist, though acknowledging Scudder could also be considered a lepidopterist or paleo-entomologist. Edwards inherited land in West Virginia, which contained rich coal deposits, and he earned his living by running a coal mine. Scudder, who married into a wealthy family, worked for the Boston Society of Natural History, as a Harvard University librarian, and a U. S. Geological Survey paleontologist (Essig 1931:758–762, Hatch 1975). They were correspondents, who sometimes agreed, sometimes disagreed. Edwards was a Darwinian, but Scudder, who had studied under, and worked for Louis Agassiz, was not, for years, but finally accepted the new biology. In *The Butterflies of North America*, James Scott began with the comment (1986:v): “In the last century William Henry Edwards and Samuel H. Scudder actively studied the natural history of many eastern U.S. butterflies, but since that time very little information on butterfly natural history has found its way into books...” (Fig. 13).

Both entomologists were very productive in research and publications, Scudder especially so. A culmination of their work was Edwards’ *The Butterflies of North America* (three volumes, 1868–97), each volume issued originally in parts (Calhoun 2013); and Scudder’s *Butterflies of the Eastern United States and Canada* (three volumes, 1888–89). Edwards was first to systematically raise butterflies from eggs to adults and describe and illustrate each stage, indicating, when he could, food plant species of caterpillars. He influenced Scudder to attempt to do likewise. Edwards was also first to illustrate in color all species, and he first described species in which the sexes were of different colors (refuting the assumption that they were different species). Scudder published the first paper (1887) tracing the introduction and spread of an invasive European species (cabbage butterfly). Both naturalists enlisted the help of amateurs in collecting information and specimens for their books.

Londoner Conway Lloyd Morgan (1852–1936) had a rather general education and general career as an educator until he went to University College, Bristol, in 1884, where he remained (Field 1949, Klopfer and Hailman 1967:14–19, Gray 1968:381–383, Clarke 1974, Thorpe 1979:24–30, Singer 1982:265–266, Singer 1982:267–268, Boakes 1984:see index, Burkhardt 2005:see index, Bircham 2007:336–339, Birkhead 2008:see index, Birkhead et al. 2014:see index). In 1884 his career gained focus when he read Romanes’ *Animal Intelligence* (1882), with which he disagreed. Thorpe (1979:26) considered Morgan as having made outstanding contributions to both comparative psychology and ethology. He was an early experimenter in comparative psychology, and his contributions were published in 14 books, of which, at least six were relevant to ethology: *Introduction to Comparative Psychology* (1884), *Animal Life and Intelligence* (1890–91), *Habit and Instinct* (1896), *Animal Behaviour* (1900), *Instinct and Experience* (1912), and *The Animal Mind* (1930) (Fig. 14).

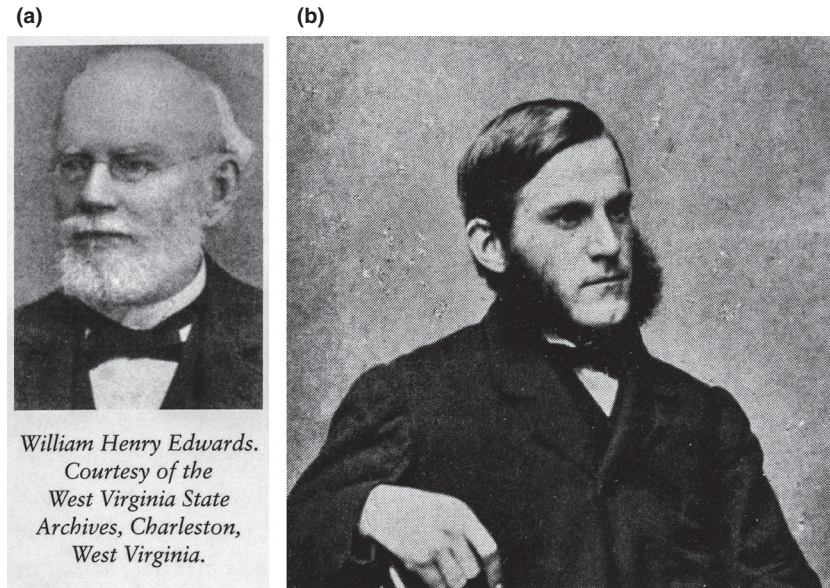


Fig. 13. (a) William Henry Edwards. Mallis 1971:288 [Leach 2013:8] (b) Samuel Hubbard Scudder. Howard 1930:plate 3.

Another Londoner, Edmund Selous (1857–1934) was similar to Fabre in that he was a loner who distained the ornithological establishment, though his education was in law, not in biology as Fabre’s was (Thorpe 1979:30–33, Durant 1981:177–180, Burkhardt 1990c, 2005:see index, Bircham 2007:336–339, Birkhead 2008:see index, Birkhead et al. 2014:see index). He began full-time bird study in 1898, publishing his first paper on the breeding behavior of nightjars (1899). Selous was a Darwinian, but unorthodox. He thought a flock’s synchronized flight was due to “collective thought,” first discussed in his *Bird Watching* (1901) and more so in his *Thought-Transference (or What?) in Birds* (1931). A summation of his studies was his *Evolution of Habit in Birds* (1933).

Danish schoolteacher Hans Mortensen (1856–1921) was responsible for introducing bird banding (“ringing” in Britain) as a standard procedure for studying birds (Preuss 2001). He attended the University of Copenhagen, but left without a degree to teach school. In 1887 he received university recognition for an essay on Danish reptiles, and in 1888 he became teacher of natural history at the cathedral school of Viborg. He was the first known Dane to take students on field trips. On June 6, 1890 he caught two starlings *Sturnus vulgaris* in one of his bird houses and placed thin zinc rings with date and location engraved on the rings. However, he concluded the rings were too heavy, and his regular banding only began on June 5, 1899, when he had obtained aluminum bands with inscriptions. That summer he banded 165 starlings, almost all adults. During the next six years he banded 1550 birds and received feedback from others who found his banded birds, which indicated migratory routes. The expenses were more than he could afford on his teacher’s salary, and he applied in 1906 to the Carlsberg Foundation for a grant, which he received then and also again in 1907, 1909, 1911, and 1921. By 1902, the practice of bird banding had spread to the United States and Germany (Lincoln 1933:66–67).

Ernest Evan Thompson (1860–1946) was born in a seaside town, South Shields, England, and his family immigrated to Canada when he was 6 years old (Wiley 1954, Keller 1984, Anderson

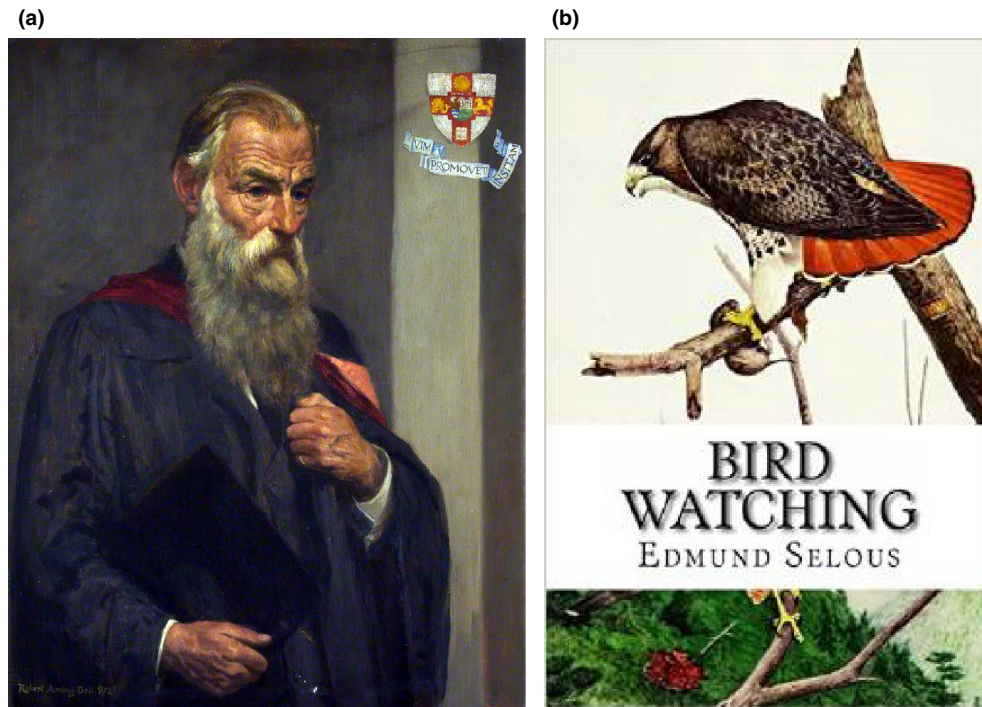


Fig. 14. (a) Conway Lloyd Morgan. Web. (b) Edmund Selous. Web.

1986, Witt 2010). Later, he added a family name, Seton, to his last name—Seton-Thompson—and still later he transposed these names to Ernest Thompson Seton. The Thompsons settled on a forested farm in western Ontario, but after four years gave up and moved to Toronto. However, during those four years Ernest became fascinated by Canada’s wildlife, and in Toronto he found others who shared his interests. He aspired to go to a university, but he got TB, dropped out of school, and never went back. He became a skillful wildlife artist, and in 1876 he became an apprentice to a Toronto artist and studied at the Ontario School of Art. He won a gold medal at a school contest. In 1879 he sailed to England and submitted a drawing to the Royal Academy of Arts for a scholarship, which he did not receive. He frequented the British Museum’s library, where he studied the works of Alexander Wilson and Audubon. In 1880 he submitted another drawing to the Royal Academy and won a scholarship, and began his studies there in January 1881. He returned to Toronto in October and later joined two brothers who were homesteading in Manitoba. He was more interested in wildlife than in farming and began publishing stories on behavior of animals he observed. He published *Fauna of Manitoba* (1886) and became Official Naturalist to the Government of Manitoba (Fig. 15).

Most of Seton’s writings—31 books and numerous articles—were of a popular nature (Seton 1954), at the time of a “nature faker” controversy. The historian of that controversy, Ralph Lutts, commented (2001:34):

Seton and [Charles] Roberts were both Canadians, and the animal story they created has been called a distinctly Canadian form of literature.... Where the nature literature of the United States focused on the human experience, this new Canadian approach focused on the animal experience.

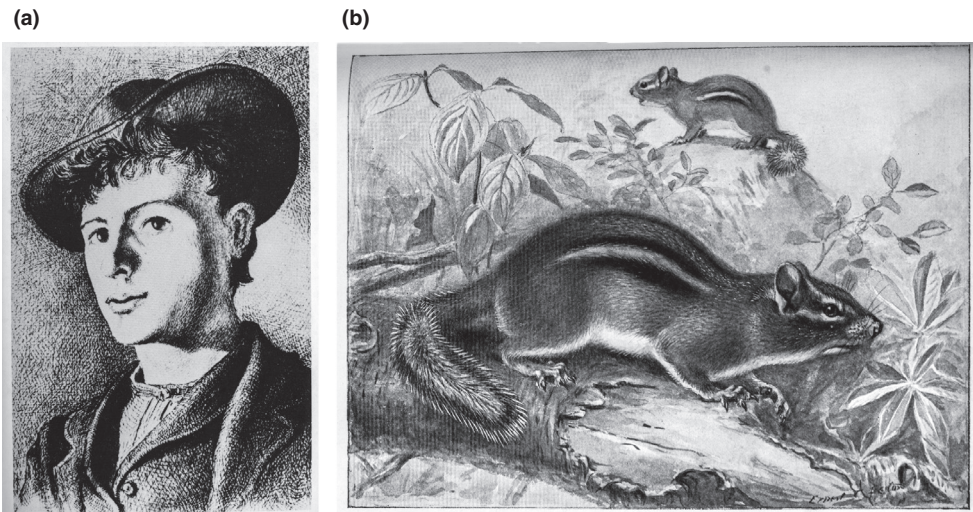


Fig. 15. (a) Ernest Thompson Seton. Self portrait. From Keller 1984: (b) Eastern chipmunk *Tamias striatus*. Seton 1925-28:IV, part 1, 186.

Noteworthy for ethology was Seton's *Lives of the Game Animals* (4 volumes in 8, 1925–28), on mammals. This work won the John Burroughs Bronze Medal from the John Burroughs Memorial Association in 1927 and the Daniel Giraud Elliot Medal from the National Academy of Sciences in 1928. *Lives* fully used Seton's artistic talent, even including some of his animal cartoons. He also included animal photographs. Modern readers will be surprised that he considered chipmunks to be game animals, but he did not consider it necessary to defend their inclusion. His maps of species' distributions were pretty much the work of the U. S. Biological Survey.

Ethology

Historian of biology Eileen Crist acknowledged the dependence of ethology upon earlier natural history studies, but also emphasized a difference in perspective: naturalists viewed their subjects as living beings, whereas ethologists viewed their subjects as “natural objects” (1998).

The word ethology has a Greek origin, *ethos*, and was introduced into the English language in 1656, meaning the study of character or ethics. Psychologist Julian Jaynes traced “The Historical Origins of ‘Ethology’ and ‘Comparative Psychology’” (1969). English philosopher John Stuart Mill, *A System of Logic* (1843), used ethology for “the ‘science of building character’ whilst employing the term psychology for the science of the ‘elementary laws of mind’” (Thorpe 1979:9, Boakes 1984:see index), which is very close to the original meaning. Paris Professor of Zoology Isidore Geoffroy St. Hilaire (1805–61) succeeded his father, Étienne Geoffroy St. Hilaire (discussed above) as professor at the Muséum d’Histoire Naturelle in 1841 (Bourdier 1972*a,b*). In Isidore's *Histoire générale des Règnes organiques* (three volumes, 1854–62), in which he used the term *ethologie* to mean what we call ecology (Geoffroy St. Hilaire 1854-62 [1859]:II, 285, cited from Allee et al. 1949:786). However, it did not gain currency then.

English historian of biology John Durant (1981:159) divided history of ethology into three phases: (1) formative, until about 1930, when pioneering studies were undertaken, (2) classical, 1930–50, when

coherent traditions were established by Lorenz and Tinbergen, and (3) mature, since 1950, indicated by Tinbergen's *The Study of Instinct* (1951).

Publishing in English

“In Britain, Darwin's evolutionary ideas provided the inspiration for four key figures, now considered the forefathers of bird behavior research: Edmund Selous [see above], Frederick Kirkman, Eliot Howard, and Julian Huxley [see below]” (Birkhead et al. 2014:248). Kirkman (1869–1945) edited the *British Bird Book* (4 volumes, 1910–13), devoted to behavior of all British species. He conducted long-term studies of black-headed gulls, and he later became active in a new Institute for the Study of Animal Behaviour (Burkhardt 2005:98–103, Birkhead et al. 2014:see index). Englishman H. Eliot Howard (1873–1940) was another amateur naturalist, who was also a successful businessman who found time for his hobby (Nice 1933:90, Thorpe 1979:33–34, Burkhardt 2005:92–98, Bircham 2007:341–347, Birkhead 2008:see index, Birkhead et al. 2014: see index). Howard's great insight was to emphasize the importance of territory for many bird species (1920, 1929), and to persuade ornithologists to appreciate territory's significance.

A prominent American zoologist who championed behavioral studies was Professor C(harles) O(tis) Whitman (1842–1910), University of Chicago and Director of the Marine Biological Laboratory, Woods Hole (Mayr 1976, Durant 1981:167–170, Singer 1982:269, Pauly 1988:129–132, 1994, Burkhardt 1990*b*, 2005:19–33, Mitman 1992:see index, 1999, Maienschein 1999, Birkhead et al. 2014:266–267). Richard Burkhardt considered him, by 1898, to be the most influential biologist in America and an important founder of American ethology, though Whitman seems never to have adopted the term. He had a long-time interest in domestic pigeons, which he raised and studied. His research on pigeons is ethological, for he was probably first to argue that behavior is one aspect of species that can provide evidence for their evolution (Lorenz 1985:267). Whitman seems not to have thought of founding a new science, and he did research at a time when natural history flourished (Seton being prominent). He had many irons in the fire, and most of his pigeon research was published in his *Posthumous Works* (volume 3, 1919) (Fig. 16).

Milwaukeean entomologist William Morton Wheeler (1865–1937) earned his Ph.D. under Whitman and ended his career at Harvard University (Evans and Evans 1970, Mallis 1971:362–368, Shor 1976, Durant 1981:165–167, Lustig 2004:298–307, Sleight 2007:see index). In 1901 the annual *Zoological Record* had begun using ethology as a subject heading, and in 1902 Wheeler wrote an article explaining that biology needed a term to designate the study of habits. He had seen three terms for this used by various researchers: natural history, ecology, and ethology (Wheeler 1902). He explained that natural history and ecology were better used to designate broader subjects, and that ethology was best to designate study of habits (Evans and Evans 1970:213–215). Wheeler began publishing on ant ethology (1903), which led to a breakthrough (Thorpe 1979:45):

A great achievement of Wheeler in relation to animal behaviour was his discovery of the phenomenon of trophallaxis, i.e., secretions provided by some individuals and castes in the ant societies which attract and reward the attention of other individuals and castes; thus binding the colony into a whole. This discovery, which was a forerunner of the present work on pheromones in insects, brought clarity and understanding into the study of insect societies...



Fig. 16. (a) Charles Otis Whitman. Wikipedia. (b) William Morton Wheeler. About 1900. Evans and Evans 1970:120.

He announced this in “A Study of Some Ant Larvae, with a Consideration of the Origin and Meaning of the Social Habit among Insects” (1918). That paper was attacked by anti-Darwinian Jesuit myrmecologist Eric Wasmann (Evans and Evans 1970:167–170, Sleigh 2007:52–55), with whom Wheeler had had earlier disagreements. Wheeler responded energetically to critics (Evans and Evans 1970:256).

Another Whitman student had a less happy fate: Wallace Craig (1876–1954). He was interested in comparative psychology and earned his doctorate at University of Chicago in 1908, with a dissertation on behavior in ringdove pigeons, and his subsequent research was also mostly on pigeons (Durant 1981:185–189, Burkhardt 2005:33–60). He obtained employment at the University of Maine teaching psychology and philosophy (1908–22). His salary there was quite modest and there was no institutional assistance for advancing his research. In 1922–27 he held three temporary positions at Harvard, and afterwards never held another permanent position, but he continued his research until he died. His research had positive influences, including upon Margaret Morton Nice and Konrad Lorenz. Craig’s paper, “Appetites and Aversions as Constituents of Instincts” (1918) was reprinted by Houck and Drickamer (1996:276–292).

Craig was stuck during his career, and to his detriment, at the boundaries between zoology and psychology. A contemporary, psychologist Robert Yerkes (1876–1956), occupied similar territory, but always as a psychologist, and therefore more securely (Hilgard 1965, Burnham 1976, Boakes 1984:148–156, 196–197). He earned his M.A. and Ph.D. at Harvard University (1899, 1902), and then served on the Harvard faculty until 1917. He founded the *Journal of Animal Behavior* in 1911, the first such scientific journal, with the expectation that all animal behaviorists, whether zoological, psychological, or both in orientation, would publish in it (Burkhardt 1987). It was not a very successful gamble, however, for it lasted just seven years. Yerkes was President of the American Psychological Association, 1916–17. In 1924, he joined the Yale University Institute of Psychology as a comparative psychologist to study primates. In 1929, he founded an experimental station near Orange Park, Florida, later named Yerkes Laboratories of Primate Biology. He also sponsored three psychology students to study primates in the wild—gorilla and chimpanzee in Africa and howler monkeys on Barro Colorado Island, Panama (Peterson 2006:163–166). The African studies were too brief to obtain significant observations, but there was

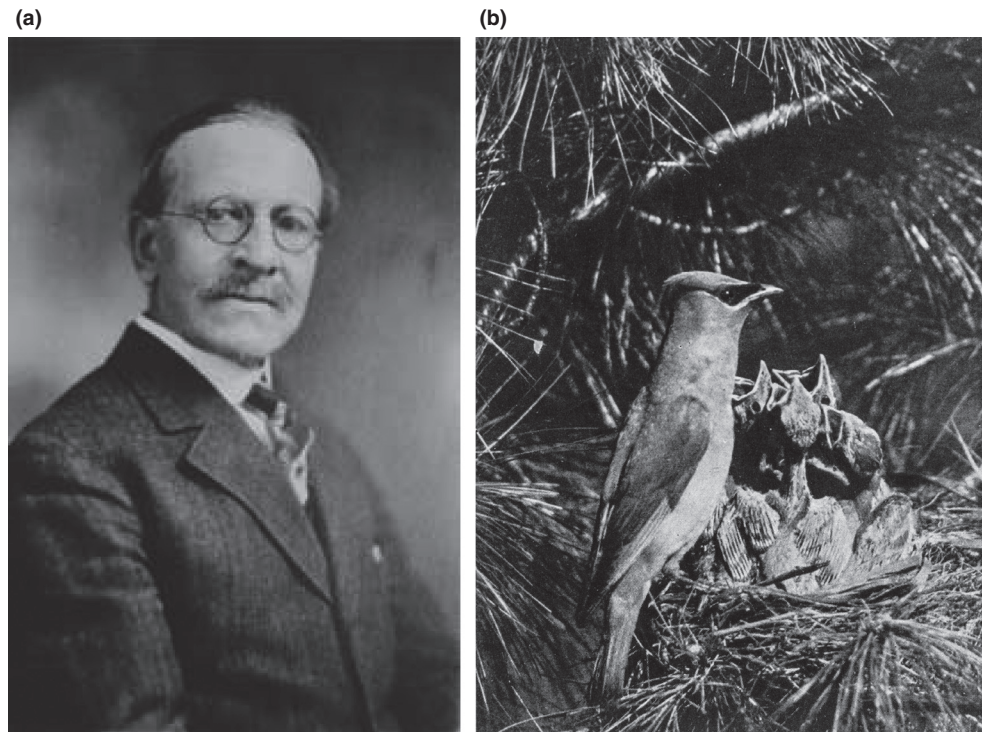


Fig. 17. (a) Francis Hobart Herrick. Web. (b) Cedar waxwing and young. Herrick 1935:frontispiece.

a biological research station on Barro Colorado Island, and Clarence Ray Carpenter studied the monkeys from 1931 to 1935 and did make substantial contributions. Yerkes did not focus upon research at Orange Park to the neglect at Yale laboratories. For example, two monographs on chimpanzees under his supervision published in 1937 were based upon studies at Yale (Cowles 1937, Crawford 1937). Yerkes retired from the directorship of the Laboratories in 1941 and from Yale University in 1944.

Vermonters Francis Hobart Herrick (1858–1940) graduated from Dartmouth College (B.A. 1881) in zoology, with an interest in marine Crustaceans (Leutner 1940). His graduate studies were at Johns Hopkins University (Ph.D., 1888), then he spent his academic career at Western Reserve University, Cleveland (retired, 1929). In 1890, the U.S. Fish Commission asked him to study the American lobster, leading to his monograph, *The American Lobster: A Study of Its Habits and Development* (1895). Microscopic studies strained his eyesight, and he switched to ornithology (Barrow 1998:187). In the same year that English ornithologist Selous's *Bird Watching* appeared (1901), Herrick published *The Home Life of Wild Birds: A New Method of the Study and Photography of Birds* (1901). He had been preceded, however, by Frank Chapman's *Bird Studies with a Camera* (1900). Herrick used a small tent as a blind, and Erwin Stresemann argued that his book marked "a turning point in the research methods of field ornithologists" (1975:342). His photographs documented nesting behavior, which Herrick judged to be entirely instinctive. He then began publishing a series of seven papers on the habits of bald eagles (listed in Nice 1979:277–278), which culminated in *The American Eagle: A Study in Natural and Civil History* (1934). The earlier book attracted the attention of Konrad Lorenz, and he and Herrick then began to correspond (Nice 1979:141). While studying eagles, Herrick also studied the nesting behavior of song birds and gulls and terns, described in *Wild Birds at Home* (1935), which includes numerous photographs (Fig. 17).

Margaret Morse (1883–1974) had a mother who had graduated from Mount Holyoke and a father who taught history at Amherst College (Trautman 1977, Nice 1979, Rossiter 1982:see index, Ainley 1987, Bonta 1991:222–231, Mitman and Burkhardt 1991:180–186, Barrow 1998:195–198, Burkhardt 1999, Birkhead 2008:see index, Birkhead et al. 2014:see index). She followed her mother’s example by graduating from Mount Holyoke College (1906). She studied for a graduate degree at Clark University for two years before marrying (1909) physiology graduate student Leonard Blaine Nice (1882–1974). While raising four daughters (a fifth died as a child), she earned a master’s degree (1915) from Clark University, with a thesis on the feeding habits of bobwhite quail *Colinus virginianus*, which she had published earlier (1910). Blaine’s first appointment was at the Harvard University Medical School (1911–13), then he joined the faculty of the University of Oklahoma (1913–27). In early August, 1919, Margaret read in the *Daily Oklahoman* that state game warden Ben Watts advocated opening the state hunting season on mourning doves in August, since the young were (supposedly) flying by then (Nice 1979:42). She doubted this, and on August 20, she found three dove nests on campus containing young. She notified the *Daily Oklahoman*, the Oklahoma Game Department, and the U.S. Biological Survey and defeated Watts’ proposal. That act was the beginning of her career as an ornithologist and ethologist. She also raised several pet mourning doves. While living in Norman, she and Blaine collaborated to publish *The Birds of Oklahoma* (1924). They next moved to Ohio State University (1927–36), in Columbus, where in “Theory of Territorialism and Its Development” (1933:89), she cited, from a similar article by W. Meise (1930), early discoveries by Johann F. Naumann (1820) and Bernard Altum (1868). (One of her supporters and advisors, Ernst Mayr, subsequently published “Bernard Altum and the Territory Theory” [1935]).

Nice’s main behavioral studies were on song sparrows *Melospiza melodia*, which studies she mainly conducted in Columbus (Nice 1937, 1967). While she visited Berlin in 1932, Mayr introduced her to Erwin Stresemann, and she commented upon her difficulty in having a lengthy study published in American ornithological journals. He offered to publish her study in the *Journal für Ornithologie*, which he edited (Nice 1979:115–116). She accepted, and so her first article on song sparrows was translated into German by Dr. Herman Desselberger and appeared in two parts (Nice 1933–34). By then, she had read Konrad Lorenz’s 60-page article in that journal, “Beiträge zur Ethologie sozialer Corviden” (1931), and he had read her article on song sparrows. They met at the 8th International Ornithological Congress, Oxford University, July 2–6, 1934, and became friends. In the “Forward” to her autobiography, he recalled: “I was at once impressed by her deep understanding of ethology, its methods and its approach” (1979:ix). She apparently first met Niko Tinbergen at the 56th annual meeting of the American Ornithological Union in Washington, 17–22 October 38 (Nice 1979:197).

Nice’s personality and achievements provided inspiration for two well-illustrated, though brief, books for teens: Julie Dunlap’s *Birds in the Bushes* (1996), being a biography, while Michael Ross’ *Bird Watching with Margaret Morse Nice* (1987) is a “how-to” book, using her example as a model for one’s own studies. Nice’s studies on the behavior and song of song sparrows also inspired others to continue such studies (Searcy and Nowicki 1999) (Fig. 18).

Indianan Warder Clyde Allee (1885–1955) was from a Quaker community near Bloomingdale, and he attended Quaker-supported Earlham College, Richmond, Indiana (Schmidt 1957, Banks 1985, Mitman 1992:see index, Dugatkin 2006:37–60, Egerton 2015a:46). He taught biology and geology at a nearby high school, 1907–10, then entered the graduate zoology program at the University of Chicago, where he earned his MS. and Ph.D. in zoology (1910, 1912) under ecologist Victor Shelford. He then

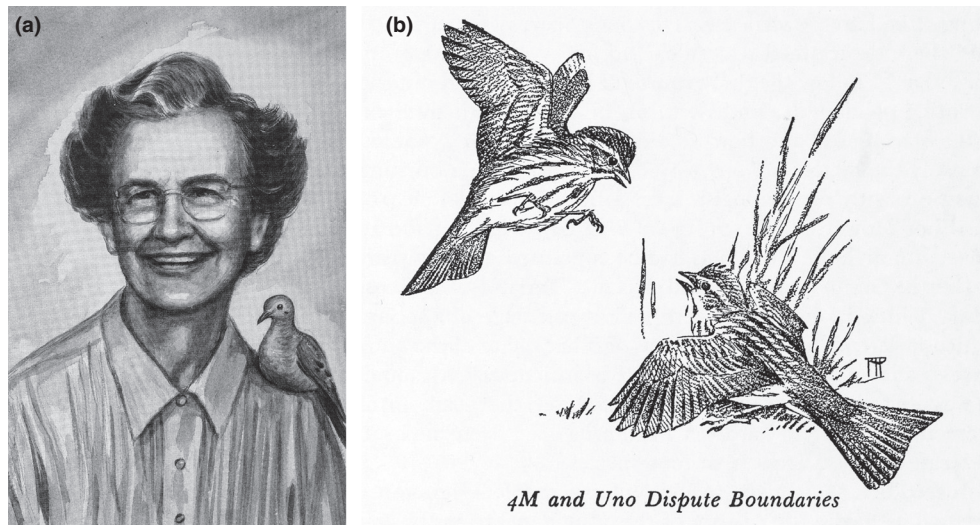


Fig. 18. (a) Margaret Morse Nice, with a pet mourning dove. Drawn by Ralph L. Ramstad for frontispiece in Dunlap 1996, based upon photo reproduced in Ross 1987:4; photo lacks pet dove. (b) Male song sparrows 4M and Uno dispute boundaries. By Roger Tory Peterson. Nice 1939:5.

taught at four different universities before returning to the University of Chicago in 1921 and remained for 29 years before forced retirement. At Chicago he taught a course and a graduate seminar in animal behavior, and published *Animal Aggregations* (1931), *Animal Life and Social Growth* (1932), *Cooperation among Animals* (1938, edition 2, 1951), became senior author of Allee et al., *Principles of Animal Ecology* (1949), which included a bibliography of his articles.

Englishman Julian S. Huxley (1887–1975) was the grandson of the illustrious Victorian, Thomas Henry Huxley (1825–95), “Darwin’s Bulldog,” who had also been interested in behavior (Boakes 1984:see index). Julian’s life perhaps rivaled his grandfather’s, except that his fame became even more international (Baker 1976, Olby 2004). Julian Huxley had become interested in birds when he was eight, and at age 13, he saw a green woodpecker, which inspired him to learn “the language and habits of birds” (Huxley 1970–73:1, 26, 40). His developing interest in bird behavior coincided with publication of ornithological literature featuring that same perspective (Klopfer and Hailman 1967:36–38, Durant 1981:181–184, Burkhardt 1992:129–131, 2005:see index). His most remembered ethological study was on the mating of great crested grebes *Podiceps cristatus* (1914), in which (Baker 1976:213):

He established that there were three separate types of sexual ceremonies, namely (1) those that took place at the time of ‘pairing-up’; (2) those connected with the act of coition; and (3) those performed by both birds of a pair simultaneously, after pairing-up, without relation to coition (Fig. 19).

South African Solly Zuckerman (1904–93) studied anatomy at Cape Town University and in 1926 immigrated to London, where he was employed to make post-mortem examinations on deceased animals (Zuckerman 1970–88). He had begun studying baboons in Africa and continued doing so in London, which resulted in *The Social Life of Monkeys and Apes* (1932). He believed that his baboon findings were broadly valid for other primates as well.



Fig. 19. (a) Julian S. Huxley. Web. (b) Courtship of great crested grebes. Photo, H. Arndt, at Lübeck, Germany. From Immelmann 1977:9.

David Lack (1910–73), discussed in part 55 of this history, on animal population ecology (Egerton 2015b), deserves mention here on ethology (Tinbergen 1973, Thorpe 1974, Burkhardt 2005:see index). He played an important role as skeptic of the hypothesis by Verro Wynne-Edwards (1906–97), that the behavior of some species of birds limits the growth of their population by the territorial requirements of nesting pairs, also discussed in part 55 (Wynne-Edwards 1985, 1986, Leigh 2010). Neither McGill (1965) nor Houck and Drickamer (1996) included a selection from either Lack or Wynne-Edwards in their sourcebooks on ethology.

Ethologist Niko Tinbergen, whose early career was in the Netherlands (see below), thanks to Lack's influence, was invited to move to Oxford University in 1949 (Kruuk 2003:154, Burkhardt 2005:295). After Tinbergen's arriving, Dr. William Thorpe consulted with him and others to organize a symposium at Cambridge University, "Physiological Mechanisms of Animal Behaviour" (July 1949)—sponsored by the British Association for the Study of Animal Behaviour and Society for Experimental Biology—to which symposium two zoologists each from The Netherlands, Germany, and the United States were invited (Thorpe 1979:81–82). Tinbergen's perceptive biographer, Hans Kruuk (2003:147), judged this meeting as "a climactic event for Niko," where he was reunited with Konrad Lorenz for the first time since World War II. The physiologists who attended were less than enthusiastic with the new ethological science. Tinbergen trained ethologists at the same university as Lack was training ornithologists and Elton was training mammal population ecologists. Although he did not interact much with Elton, he did teach and advise some of Lack and Elton's students (Crowcroft 1991:61, 135, Kruuk 2003:7). Tinbergen also published possibly the two earliest surveys of ethology in English Tinbergen (1951, 1953b).

Thorpe's Cambridge symposium was a precedent for a series of international ethological conferences, the next of which was organized by German ethologist Erich von Holst at his new Max Planck Institute at Wilhelmshaven, for 30 May–5 June, 1950. Thorpe and Tinbergen were the only non-Germans



Fig. 20. Niko Tinbergen and Konrad Lorenz at Altenberg, Austria, 1978. Kruuk 2003:273.

among the dozen participants (Burkhardt 2005:374). The First International Symposium of Comparative Behavior Researchers met at Buldern, Germany in 1952. Others symposia followed (Fig. 20).

By 1953 (Lehrman 1953), after Lorenz had regained his prewar prestige, his ethology was subjected to a serious critique by New York City native Daniel S(anford) Lehrman (1919–72). Lorenz later summarized his understanding of Lehrman’s critique Lorenz (1985:278–279):

Lehrman dismissed, in principle, the existence of innate movement patterns and, in so doing, supported his argument substantially by using a thesis of D. O. Hebb, who had maintained that innate behavior is defined only through the exclusion of what is learned and, thus, as a concept was “non-valid,” that is, unusable. Drawing on the findings of Z. Y. Suo (1932), Lehrman also asserted that one could never know whether particular behavior patterns had been learned within the egg or in utero.

Only later did Lorenz conclude that instinctive and learned behavior could not be rigidly separated, as was previously done by ethologists.

*Tinbergen published *The Study of Instinct* in 1951, though completed in 1948 (Tinbergen 1985:450–452). Retrospectively, he saw this book as containing his early discussion of “why” in science. That question continued developing in his thoughts until its ultimate expression in “On Aims and Methods of Ethology” (1963). His four “why” questions of concerned causation, survival value, ontogeny, and evolution (Hogan and Bolhuis 2009:33).*

In September, 1965, the Royal Entomological Society of London held its Third Symposium, which was on insect behavior (Haskell 1966). There were eight presenters, one from Germany, one from Canada, two from

USA, and four from UK. Seven topics were very basic: orientation, rhythms, flight, feeding, sexual, communication, and social insects; the last topic “Some outstanding Questions in Insect Behaviour,” by insect physiologist J. S. Kennedy (1966), Cambridge, UK, was a response to the symposium. Some symposium participants might have been disappointed that Kennedy chose three questions from Edward O. Wilson’s (1966) presentation on social insects, and even those three questions were aspects of group inheritance, being Wilson’s response to W. D. Hamilton’s influential “The Genetical Theory of Social Behaviour” (1964).

Illinoisan entomologist Richard D. Alexander (b. 1929) focused on insect behavior, especially in crickets (bibliography at his web site). He earned his B.S. degree at Illinois State University (1950) and his M.S. and Ph.D. from Ohio State University (1951, 1956). He spent his career at the University of Michigan, Ann Arbor, where he mentored ecologists. An example of his own contribution to insect ethology is his address to an International Conference on Systematics in 1967: “Comparative Animal Behavior and Systematics,” (1969), in which he argued that behavior is a valuable means of distinguishing between some similar species. He next began publishing on human behavior (his anthology, 2013). His earliest publication on the latter subject was a review (Alexander and Tinkle 1968) of Konrad Lorenz, *On Aggression* (1966) and Robert Ardrey, *The Territorial Imperative* (1966). In her commentary on a reprint of that review, Bobbi Low explained its larger significance (2013:125):

...this short piece foreshadows Alexander’s subtle and encompassing theory of cooperation, and the interplay between cooperation and aggression, as well as laying out, with remarkable sophistication for the time, the interactions between natural selection [and] cultural selection...

Kenyan anthropologist-paleontologist-zoologist Louis Leakey played a very unusual, important role as facilitator for three young women who wanted to study behavior of great apes. They all went to him for assistance.

First was English Jane Goodall (b. 1934), who became the most famous living student of animal behavior (Montgomery 1991:24–45, 193–213, Peterson 2006), though her work is not prominent in ethology textbooks I reviewed; Lee Dugatkin (2009) cited one of her books listed under “Goodall” and another under “Lawick-Goodall,” depending upon the name used when published; her graduate advisor at Cambridge University, Robert Hinde, cited three of her publications (under her married name, Lawick-Goodall) in his *Animal Behaviour* (1970). She was invited to write an autobiographical chapter for *Leaders in Animal Behavior* (1985; Drickemer and Dewsbury 2009:vii), but declined because she had already published autobiographical accounts. In 1962, she participated in a symposium sponsored by the Zoological Society of London, and reported on her 2 years of chimpanzee observations, emphasizing her discovery of predation and tool use (Peterson 2006:290–292). Zuckerman chaired the symposium and decided that her claim of observing carnivorous chimpanzees contradicted his 1932 claim that all primates were vegetarians. His *The Social Life of Monkeys and Apes* was a capable synthesis for 1932, but instead of welcoming her discovery, he discounted her claim (Zuckerman 1962, 1988; on his status as a primatologist: Burt 2006). Goodall subsequently earned a Ph.D. in ethology at Cambridge University (1965), under Hinde, following an atypical academic route. One feature that distinguishes her work is a half century of diligent observations and publications (Goodall 1965, 1967, 1971, 1986, 1990, 2010). However, she had a steady stream of assistants, mostly students who came for varying periods, whose chimpanzee observations enabled her to leave Gombe for various reasons, while still maintaining control. Students were assisted by native workers. Her research was funded mostly by National Geographic



Fig. 21. (a) Jane Goodall. Goodall 2010:28 or 40 or 75. (b) Dian Fossey. Fossey 1972:208.

Society, Washington, D.C. during the 1960s, with other funds becoming available afterwards, including speaker fees from her numerous tours in the United States (Fig. 21).

Two noteworthy collections of studies on primate behavior appeared in the United States in mid-1960s, with international contributors (DeVore 1965, Altmann 1967). Goodall (1965) contributed one of two papers on chimpanzees, the other being by other English investigators, Reynolds and Reynolds (1965).

American Dian Fossey (1932–85), was older than Goodall but started later, planning her work on African gorillas with Leakey in 1966 and establishing her Karisoke Research Centre in Rwanda in 1967 (Mowat 1987, Montgomery 1991:46–66, 214–233, Schafer 1999). She studied three groups of gorillas, and she became obsessed with protecting them from poachers. She followed Goodall’s example of enrolling for a Ph.D. at Cambridge University under Hinde, in 1970, and earned a Ph.D. in 1976. Fossey wrote a chapter, “Living with Mountain Gorillas” Fossey (1972), in the National Geographic’s *The Marvels of Animal Behavior*. She was asked to write the chapter because the National Geographic Society had funded her research. Her chapter was a very well-illustrated progress report on her studies since 1967, and she published a more definitive *Gorillas in the Mist* in 1985. She was murdered in her cabin in 1985, and her assassin was never identified.

German-born American Biruté Galdikas (b. 1946) arrived in Borneo in 1971, where she has resided ever since (Montgomery 1991:3–23, 234–255, Galdikas 1995). Besides studying orangutans in natural habitat, she runs an orphanage for young orangs who are eventually returned to the wild. She married a Borneo native.

Publishing in French

Swiss naturalist-psychiatrist Auguste Forel (1848–1931) had a life-long fascination with ants, but nevertheless decided upon a medical career (Forel 1937, Pilet 1972, Tort 1996, Lustig 2004:285–291,



Fig. 22. Auguste Henri Forel as a medical student. Forel 1937: facing 128.

Sleigh 2007:21–37). His interest in ants, as in medicine, focused on behavior, but without neglecting ant systematics. He carried on a long Swiss tradition of studies on ants, stretching back to Charles Bonnet (1720–98) (Sartori and Cherix 1983, Sleigh 2007:25). At age 25 he published *Les Fourmis de la Suisse* (1873). He sent a copy to Charles Darwin, who thanked him for it in a letter of September 28, 1874, and after reading it, Darwin wrote again (15 October 74), with high praise, that “seldom in my life have I been more interested by any book” (2015:480, 498). One of a number of Darwin’s comments compared Forel’s observations with those of Fritz Müller (1822–97), living in Brazil, on termites, in the first volume of his *Beiträge zur Kenntniss der Termiten* (1873) (on Müller: McKinney 1974). Forel’s book also exerted a strong influence upon Espinas’ *Des Sociétés Animales* (Sleigh 2007:74). Forel’s expertise was so widely respected that some collectors of ants in foreign countries had him describe species which they had collected. In 1893 Forel retired from the University of Zurich Medical School in order to devote time to studying ants. Richard tells us (1973:483) that Forel first reported (before 1900) mouth to mouth exchange of food between ants (later named trophallaxis), though others explained its significance (after 1900). Forel published *The Senses of Insects* (1908) in English, followed by a German translation (1910). Forel’s lifetime studies culminated in his monumental *Les Monde social des Fourmis compare à celui de l’Homme* (5 volumes, 1921–22, English, 1928) (Fig. 22).

Publishing in German

The term *ethology* gained some early usage in Germany, as in the title of an article by ornithologist Oskar August Heinroth (1871–1945), “Beitrag zur Biologie, namentlich Ethologie und Psychologie der Anatiden” (1911). Heinroth did not envision establishing a new science (Stresemann 1951:see index, Stresemann 1975:see index, Heinroth 1971, Durant 1981:163–165, 170–174, Burkhardt 1990b, 2005:see

index, Birkhead 2008:116–117), but his disciple, Konrad Lorenz, did. Heinroth earned a medical degree in 1895 and then studied zoology at Friedrich Wilhelm University, Berlin. He held several zoological positions and served as president of two zoological societies. He was a pioneer German student of bird behavior, and Schulze-Hagen and Birkhead (2015) argued that his three major contributions have been largely overlooked: (1) he conducted comparative studies of social signals and other behaviors in waterfowl, and recognized that their ritualized displays could serve as taxonomic criteria; (2) with his first wife, Magdalene (died 1932), he published a classic *Die Vögel Mitteleuropas in allen Lebens- und Entwicklungsstufen* (four volumes, 1924–33), drawing upon their knowledge from raising 1000 individuals of 286 species, documenting and photographing their development; and (3) he provided a framework for studying behavior throughout life, partly based upon individuals raised. He also published his discovery that when humans raised birds from eggs, they imprinted on humans (Fig. 23).

Vienna native, Karl von Frisch (1886–1982) came from an academic family, with university professors in the families of both parents, and he and his three brothers continued that tradition (von Frisch 1967:1–20). He was pleased that his mother allowed him to keep in their house his pets: nine species of mammals, 16 species of birds, 26 of cold-blooded terrestrial vertebrates, 27 of fish, and 45 species of invertebrates! His father, a professor of medicine, wanted him to study medicine, as a safer avenue for supporting himself than zoology. He did for two years, after which his father agreed he could switch to zoology. Later, Frisch found that his medical training was advantageous to him as a widely trained zoologist. Ethologists regard his discovery of the language of bees as the most important contribution to understanding animal behavior during the 1900s (Burckhardt 1990a:312, Raffles 2010:171–200).

Frisch did not immediately zero in on honey bees. He first studied ability of some fish species to change color to blend in with their background. In 1911, he encountered the claim by an ophthalmol-

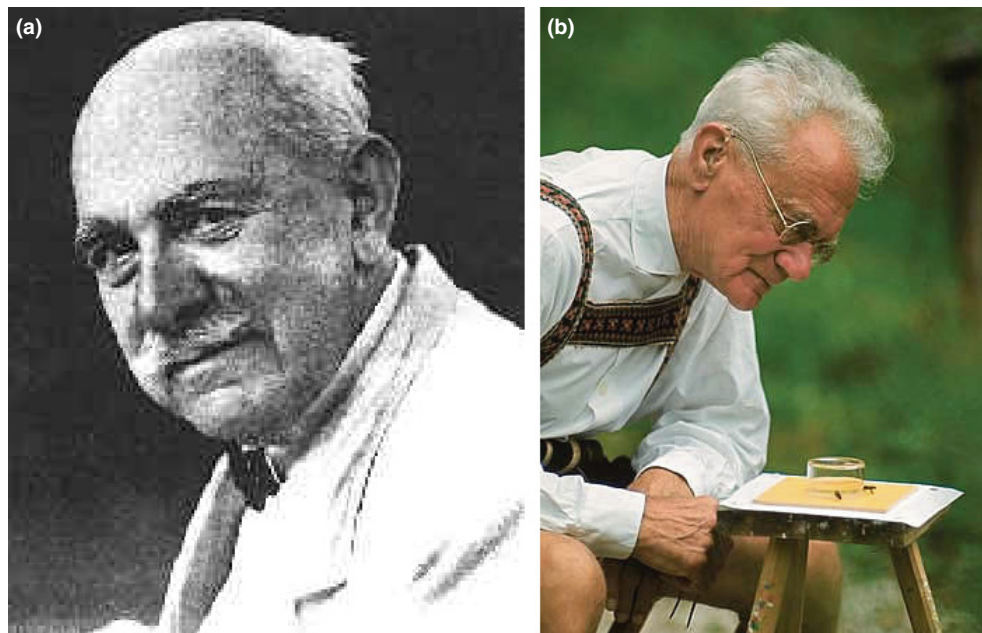


Fig. 23. (a) Oskar Heinroth. Web. (b) Karl von Frisch viewing color vision experimental apparatus for honeybees. Tinbergen and Editors, Time-Life Books 1965:20.

ogy professor and director of an eye clinic that fish and all invertebrates are color blind (von Frisch 1967:48). That challenged his experience with fish, and he also assumed that the bright colors of flowers were to attract collectors of pollen and nectar, that simultaneously pollinated flowers. To prove it, he began experimenting on honeybees during warm weather to see if they could distinguish colors. (In winter he continued experiments on fish: von Frisch 1941). Gradually, during the next nine years, he gained further insights into bee behavior and finally could explain the “speech” of bees (Frisch 1920–23). He was not content, however, to merely announce the purpose of honeybee wagging; he spent 26 years investigating the intricacies of this phenomena (Lindauer 1985:129). He was glad to explain his discoveries to others, and he went on lecture tours in America in 1930 and in 1949 (von Frisch 1967:111–116, 157–169). The lectures he gave at Cornell University during his second trip were published as *Bees: Their Vision, Chemical Senses, and Language* (1950). Nor were his ethological investigations limited to fish and honeybees. Assisted by his son, Otto, he wrote *Animal Architecture* (1974), in which they surveyed the animal kingdom concerning building abodes. However, honeybee language was his major contribution, and others have continued that research (Michelsen 1999) (Fig. 24).

Another Viennese, Konrad Lorenz (1903–88), like Frisch, was son of a professor of medicine, and his parents also allowed him to keep many animals as pets (Evans 1975, Nisbett 1976, Thorpe 1979:see index, Durant 1981:174–177, Lorenz 1985, Bateson 1990, Chavot 2000, Taschwer and Föger 2003, Burkhardt 2005:see index, Birkhead 2008:see index, Birkhead et al. 2014:see index). The wide variety of animals which Lorenz raised is indicated in his very popular *King Solomon’s Ring: New Light on Animal Ways* (1952). Lorenz’s ethological studies evolved out of his early experiences of raising animals as pets. His father wanted him to study medicine, as his much older brother had, but unlike Frisch, who had switched to zoology after 2 years of medical study, Lorenz persisted and obtained an M.D. degree, but then also studied for a Ph.D. in zoology. He was especially attracted to ducks and geese, and as he raised them from hatchlings, he discovered that they became imprinted on him as their parent. Lorenz thus independently discovered imprinting. He had that ethological methodology in common with Heinroth, whose disciple he became. Their interactions are documented in their correspondence during the 1930s (Heinroth and Lorenz 1988), which years Alec Nisbett (1976:43) thought were also the years in which Lorenz’s “most powerful scientific papers” were written. W. H. Thorpe (1979:67–68) seemingly agreed, citing five crucial papers which Lorenz published in 1931, 1935, 1937, 1939, and 1941. Reading those papers motivated Thorpe to become an ethologist. The first volume of Lorenz’s *Studies in Animal and Human Behaviour* Lorenz (1970–71) translated papers published in 1931, 1935, 1937, 1938, and 1942 (Fig. 25).

The *Deutsch Gesellschaft für Tierpsychologie* was organized in 1936, and in 1937 it founded *Zeitschrift für Tierpsychologie*, with Lorenz and Otto Koehler as editors. The Institute for the Study of Animal Behaviour was also organized in 1936, in Britain, and published the *Bulletin of Animal Behaviour*, 1938–51. In 1948, Tinbergen founded *Behaviour* as an ethological journal. *Zeitschrift für Tierpsychologie* had ceased publication during the war (Burkhardt 2005:284–285).

Publication of Lorenz’s paper on imprinting (1935) impressed Niko Tinbergen, who wrote to Lorenz expressing his interest in it. Their correspondence, and then interactions, led to their establishing a formal science of ethology (Burkhardt 2005:199). Tinbergen accepted Lorenz’s invitation to spend 1938 at Lorenz’s home at Altenberg, which was especially fruitful for both.

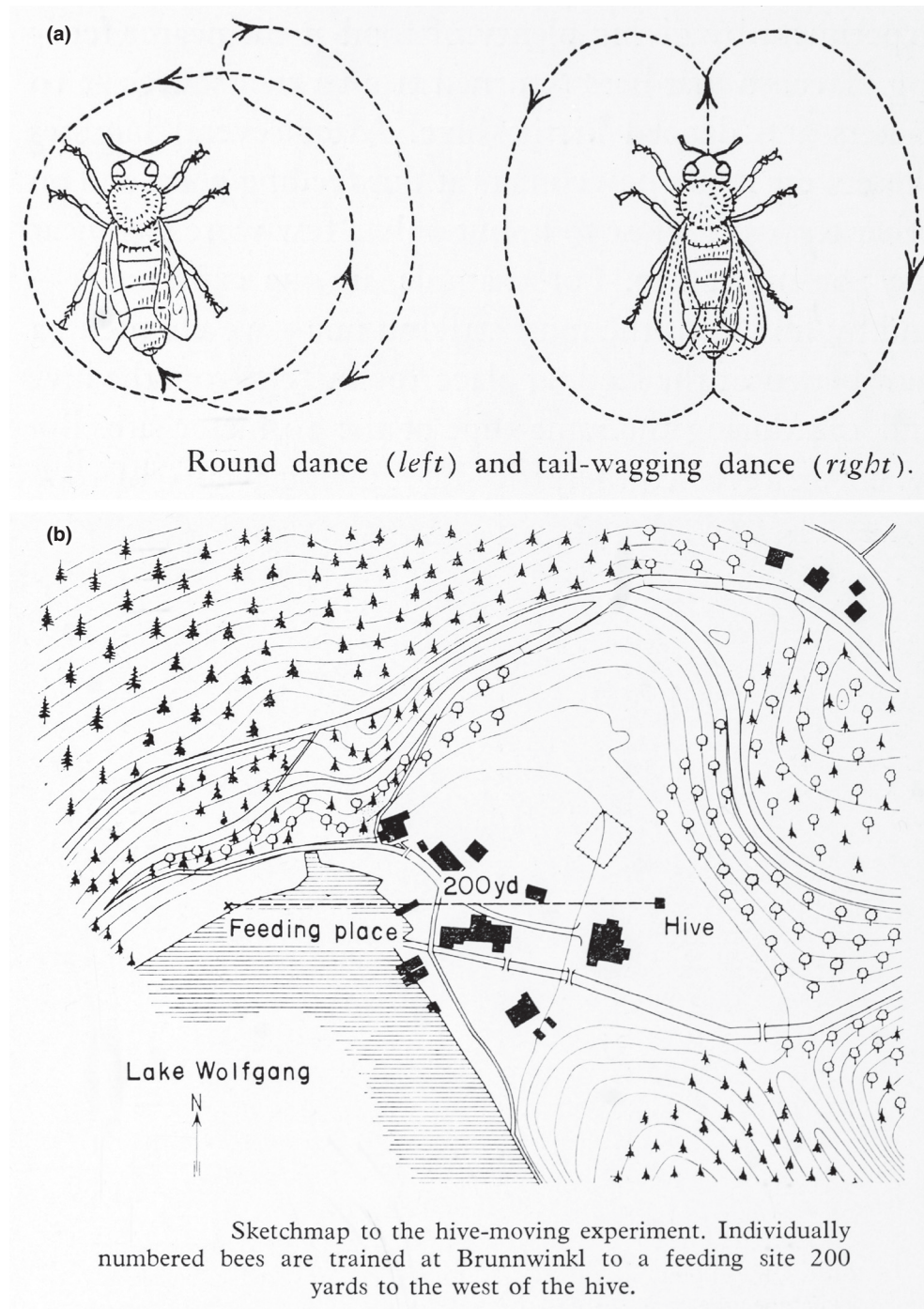


Fig. 24. (a) Karl von Frisch's diagram to illustrate bee communication. von Frisch 1966:115. (b) Diagram illustrating experiments concerning honeybee language, reprinted in his autobiography. von Frisch 1967:154.

In March 1940, Germany invaded Austria, met no resistance, and absorbed Austria into Germany. Lorenz was enthusiastic about the Anschluss and joined the Nazi party, believing its biologically tinged ideology was compatible with his biological research (Kalikow 1983, Burkhardt 2005:231–280). In 1940, Lorenz became professor of psychology at the University of Königsberg, but was drafted into the



Fig. 25. Konrad Lorenz swimming with imprinted snow geese. From Tinbergen and Editors, *Time-Life Books* 1965:17.

German Army in 1941, and as a member of the Nazi Party was sent to Poznan to study “German-Polish half-breeds” to determine if they were fit to reproduce superior German citizens (Nisbett 1976:77–91, Taschwer and Föger 2003:112–131). He became a Russian prisoner of war, 1944–48. After Tinbergen had been persuaded to move to Oxford in 1949, Thorpe decided to bring Lorenz to Cambridge (Thorpe 1979:123). However, in 1950, the Max Planck Society moved quickly to establish the Lorenz Institute for Behavioral Physiology, which kept him in Germany, and from which he retired in 1973, though continuing his research, lecturing, and writing. Thorpe continued his comments (Thorpe 1979:69): “the fact that Lorenz’s early papers now appear so outdated is a tribute to their effectiveness.” Lorenz himself was among the ethologists whose researches rendered his earlier papers outdated. The second volume of his *Studies in Animal and Human Behaviour* contained papers published 1941–63. Four Lorenz papers which Richard Evans republished [1975:129–269] had appeared in 1966–70. Lorenz’s *The Foundations of Ethology: The Principal Ideas and Discoveries in Animal Behavior* (1981, German, 1978) was a synthesis of what he and some others had achieved.

Nicolaas (“Niko”) Tinbergen (1907–88) was Dutch, but is placed here among German speakers because a number of his early publications were in German and his early ethological interactions were with Konrad Lorenz (Thorpe 1979:see index, Tinbergen 1958, Tinbergen 1985, Dewsbury 1990, Kruuk 2003, Burkhardt 2005:see index, Bircham 2007:386–394, Birkhead 2008:see index, Bolhuis and Verhulst 2009, Birkhead et al. 2014:see index). Niko’s father was not a professor of medicine, as Frisch and Lorenz’s fathers were; his father taught high school in The Hague, but he did have a Ph.D. and was a respected scholar of Medieval Dutch literature, and the Tinbergen home was as intellectually oriented as those of Frisch and Lorenz—Niko’s older brother, Jan, won a Nobel Prize in economics (1969). Being

uncertain of a career when he completed secondary school in 1925, his parents sent him to a field station in Germany for two months, where he learned bird banding and nature photography (Kruuk 2003:33–35). That experience convinced him to study ethology at Leiden University (Fig. 26).

Only, Leiden University did not teach it. He had to study biology, and in the fourth of a five-year program he could begin to specialize (Kruuk 2003:38–39). That being the case, he conducted his own nature studies outside formal courses. In early 1929, a friend, Martien Rutten, son of a geology professor at Utrecht University, invited him to join his family on a skating party on the Zuiderzee Inlet, which Niko readily accepted. There he met Martien's young sister, Elizabeth ("Lies"); they fell in love, and married in 1932. Although strongly interested in birds, Tinbergen decided to continue an earlier project on bee-wolf wasps *Philanthus triangulum* for his doctoral research (Tinbergen 1969:1–18, Ph.D., Tinbergen 1932). Three of his early ethology papers (1932, 1935, 1938) were based upon his dissertation and are now reprinted in English translation in his collected papers, *The Animal in its World: Explorations of an Ethologist, 1932–1972* (two volumes, 1972).

Soon after obtaining his doctorate and getting married, he and Lies joined a Dutch government-funded expedition to Greenland for the International Polar Year, 1932–33, which had "a tremendous effect on Niko, on his outlook on life and on his science" (Tinbergen 1969:19–59; Kruuk 2003:59–69). These flatlanders found the beauty of the mountainous landscape overwhelming. Native Inuits lived by hunting seals and polar bears, and by fishing, and Tinbergen learned from them how to do the same. He studied sledge dogs, which observations were used in his book, *Eskimoland* (Rotterdam, Tinbergen 1935). In spring and summer, he studied snow buntings, which English ornithologist Max Nicholson had previously studied in Greenland and concluded they were not territorial. Tinbergen discovered that he was mistaken, because he had studied them at the wrong time of year. Snow buntings were subjects of a long-term study, but Tinbergen also devoted three weeks to red-necked phalaropes, in which females are brightly colored and dull-colored males incubate eggs. He found that females also defended territories. Tinbergen's biographer claimed that his Greenland experience transformed him from a "sentimental naturalist to a hunter who saw his animals as objects" (Kruuk 2003:69).

In May, 1940, Germany invaded the Netherlands, yet Tinbergen's life did not change much during the first two years of occupation, except that he and Lies turned their house into a hospital (Kruuk 2003:114).



Fig. 26. Niko Tinbergen examining a common tern *Sterna hiundo* killed by a fox, at Ravenglass, England. Tinbergen & Editors of *Time-Life* 1965:32.

Leiden University, however, became uncooperative with German demands, such as expelling Jews, and was closed. Trains became sabotaged and German soldiers were shot. The Germans responded by arresting 1900 public figures as hostages, which included Tinbergen. 1400 of them, including him, were kept in a commandeered Catholic college, Beekvliet. Inmates organized activities to escape boredom, and he lectured on Greenland and ethology.

Tinbergen's studies were methodologically different from Lorenz's. Lorenz raised free-ranging birds and studied their habits. Tinbergen observed wild birds and arranged experiments on them without interfering with their freedom (Tinbergen 1953a, 1960, 1972). In 1949, Tinbergen settled at Oxford University and then became part of the British biologist community, but with no break in his relationship with Continental ethologists (see above).

1973 Nobel Prize

Before 1973, no ecological science had received any notice to rival the prominence of other biological sciences, such as physiology or molecular biology. Nobel laureate Peter Medawar had for many years befriended and admired Tinbergen, and "he was probably the main protagonist recommending the honour for the three ethologists" (Kruuk 2003:268). The award required a broadening of the scope of the prize for physiology and medicine. In 1973, Frisch was 86 and unable to go to Stockholm for the ceremony, Lorenz was 69, and Tinbergen 66. Frisch received the award for his discovery of language of hive bees, Lorenz for being "acknowledged founder of the science of ethology," and Tinbergen for having "brought the new science of ethology into full flower" (Marler and Griffin 1973:464; Nisbett 1976:220–223, Feldman 2000:280–283, Kruuk 2003:268–273, Taschwer and Föger 2003:225–240, Burkhardt 2005:446–449).

Recently, Hans Kruuk commented (2003:3):

The label 'ethology' is rarely used these days. It is the science concerned with the biology of animal behaviour, and the more usual term now is just 'animal behaviour', as in 'Department of Animal Behaviour'. Aspects of ethology live on in new disciplines, in behavioural ecology, sociobiology, cognitive ethology, neuro-ethology, and others.

Conclusions

Natural history studies since Aristotle provided a wealth of information on animal behavior, but it did not add up to a coherent science of animal behavior, with hypotheses and theories. The attempt to move beyond mere information to the formation of a science of ethology began around 1900 with: British naturalists Selous, Kirkman, Howard, and Julian Huxley; American Whitman, Wheeler, Craig, and Yerkes; and German Heinroth. Their contributions were met by a receptive audience that included American Allee, Austrians Frisch and Lorenz, and Dutch Tinbergen. However, it was Lorenz and Tinbergen who formally organized the science of ethology. Early observations on hive bee dance did not contribute to a progress of knowledge because they were not within a science context. English ethologists Thorpe and Goodall and Americans Fossey and Galdikas were among the subsequent con-

tributors to ethology. Englishman Hinde and German Eibesfeldt had published textbooks on ethology by 1970. The award of a Nobel Prize in Physiology or Medicine for 1973 went to Frisch, Lorenz, and Tinbergen, the publicity of which helped move ethology into the mainstream of biological sciences.

This is primarily a chronological survey, and therefore does not constitute a full summary of the content of ethological developments. References cited can carry readers into that deeper subject.

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