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Editorial

Welcome to the 59th volume of the monograph series published by the ZFMK. The monograph series of the ZFMK has been in publication since 1971, and was until 2012 known under the name 'Bonner Zoologische Monographien' (Bonn zoological Monographs), or BZM.

In order to profit from the experience gained during the modernization of our journal series, the Bonn zoological Bulletin, or BzB, monographs will now be published as a Supplementum series to the BzB. The Supplementum series will provide a publication outlet for articles that are too voluminous and 'monographical' in style to be printed in the BzB. This volume is the first example of the new Bonn zoological Bulletin, Supplementum. The transition of the BZM to a BzB Supplementum series allows the monograph series to be immediately added to the 'Directory of Open Access Journals'. We hope that in the future the Supplementum will achieve an impact factor. Both improvements would not be possible using the former monograph format.

The Supplementum series will be free of charge to the authors, and all recent issues, as well as volumes 55–58, will be accessible online. In the future, we hope to put all past BZM issues in a freely available online archive, which will further enhance the visibility of and access to our publications.

This volume has a changed layout and design, to better fit the style of our BzB journal series. We thank Eva-Maria Levermann for her professional layout work and Uwe Vaartjes for the design of the new cover.

The first contribution to the monograph series in its new format was written by Jürgen Haffer, Hans Hudde and Brian Hillcoat. Until his death, Jürgen Haffer served as a long-time member of the journal's Advisory Board. Brian Hillcoat also worked on numerous previous BZM issues as an editorial assistant.

We would like to thank Prof. Dr. K.-L. Schuchmann for serving as editor of the BZM from 2005–2012 and wish him the best for his upcoming retirement. We hope that the transition of the BZM to the BzB-Supplementum series continues to serve readers and authors in the best possible way.

With best wishes to all readers, the authors, and the BzB-S team,

Thomas Wesener
Managing Editor, BzB Supplementum,
Myriapoda Curator at the ZFMK
Bonn, October 2013

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The Development of Ornithology and Species Knowledge in Central Europe

Jürgen Haffer (†), Hans Hudde & Brian Hillcoat

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Bonn zoological Bulletin – Supplementum 59: 1–116 November 2013

The Development of Ornithology and Species Knowledge in Central Europe

Jürgen Haffer (†), Hans Hudde[*] & Brian Hillcoat[**]

(†) Tommesweg 60, D-45149 Essen, Germany
[*] Rüstermark 2, D-45134 Essen, Germany
[**] Humboldtstraße 34, D-14193 Berlin, Germany

Abstract. This work has two distinct aspects, as suggested in its title: an outline of the history of Central European ornithology, concluding with the worldwide influence of the "New Avian Biology" of Erwin Stresemann, and an account of development in the knowledge of European bird species illustrated by extracts from the works of selected ornithologists up to the 19th century. How this increased knowledge was reflected and refined in the gradual rise in the number of species identified and named is shown in three chronological online Appendices and many illustrations. These tables of German vernacular names will be a most useful resource for scholars studying early texts. The major figures considered regarding bird names are Hans Sachs (1495–1576), Marcus zum Lamm (1544–1606), Conrad Gessner (1516–1565), Caspar Schwenckfeld (1563–1609), John Ray and Francis Willughby (1627–1705) and (1635–1672), H.F. von Göchhausen (1663–1733), J.L. Frisch (1666–1743), J.T. Klein (1685–1759), J.H. Zorn (1698–1748), J.A. Naumann (1744–1826), J.M. Bechstein (1757–1822), and J.F. Naumann (1780–1857). As an illustration of one man's detailed knowledge of field ornithology, special emphasis is given to a detailed description of J.A. Naumann's little-known first book *Der Vogelsteller* [*The Bird-Trapper*] of 1789.

The two great research traditions in the discipline – systematic ornithology and field ornithology – arose from the works of John Ray in England, but after almost three centuries of separate development were only reunited from the early 1920s, principally in the work and influence of Erwin Stresemann (1889–1972), especially following the publication of his *Aves* in 1927–1934. This could perhaps have taken place earlier, since the "Golden Age" of ornithology in Central Europe from *ca.* 1820 to 1850 (J.F. Naumann, C.L Brehm, F. Faber) provided an excellent foundation on which to build further scientific research, especially after the publication of Charles Darwin's epochal *On The Origin of Species* in 1859. But ornithologists became "distracted" by dealing with the flood of exotic species from the colonies and from sponsored expeditions to the remotest places. Only in the early 20th century did the momentum pick up again with the late acceptance of Darwin's ideas and the work of Stresemann in Berlin. The resulting concentration on avian biology rather than systematic-faunistic studies meant that gradually the two research traditions came together again. The spread of this New Avian Biology to the U.S. and U.K. is examined in the lives and work of Ernst Mayr (1904–2005) and David Lack (1910–1973), respectively.

TRANSLATOR'S PREFACE

Just a few weeks before his shockingly sudden death in April 2010, Jürgen Haffer contacted me to inquire whether I would be able to undertake the job of translating his latest manuscript. The work was originally to appear in this journal when it published papers and longer pieces in German and English, but before he finished his German manuscript the journal's policy was changed to English only. His final illness was beginning to affect his health to such an extent that he felt he was not able to translate what he had written, something he was normally able to do better than anyone since he was completely bilingual. His manuscript stops abruptly in the "Return to ornithology" part of the section on Gloger in Chapter 6, though he also completed most of the later Discussion beforehand. The Discussion remains as he left it, followed by his own Acknowledgments.

His life was cut short before he was able to complete his task, and he had to be satisfied with leaving me a list of instructions as to how I should continue. These mostly took the form of using his own previously published material, of which there was an abundance, since the history of ornithology, in Central Europe in particular, was his speciality. The papers he directed me to, from which passages – at times lengthy – are used in the text, are Haffer (2006) *Blätter aus dem Naumann-Museum* 25: 1–55 (in the section on Tiedemann at the end of Chapter 5); Glaubrecht & Haffer (2010) *Zoosystematics and Evolution* 86: 81–115 (in the last part of the section on Gloger in Chapter 6, where the main manuscript ends); Haffer (2007) *Journal of Ornithology*, Supplement 2: S125–S153 (in Chapter 7); Haffer (2001) *Journal für Ornithologie*, Special issue 1: 27–93 (in Chapter 8), and Haffer (2008) *Archives of Natural History* 35: 76–87 (in the passages concerning David Lack, etc. in Chapter 8). One "unfortu-

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nate" result occurs in Chapter 2, in the section on the great English naturalist John Ray. Dr. Haffer translated many pages from Ray's seminal work *The Wisdom of God* (1691) into German, therefore I had no choice but to reproduce the passages word for word from the English original (the facsimile of the modern 1826 edition), an unusual and not very satisfactory situation. Nevertheless, it would have been contrary to his intentions to shorten this passage since the many examples Dr. Haffer quotes from Ray's book – one of the two key figures in his argument – not only show what a brilliant observer Ray was, but also illustrate Haffer's extremely important point that all of the behavioral and physiological phenomena exhaustively listed to show us the Wisdom of God are easily converted into today's evolutionary adaptations. As his old friend Ernst Mayr put it (Mayr 1982: 105): "When 'the hand of the creator' was replaced in the explanatory scheme by 'natural selection', it permitted incorporating most of the natural theology literature on living organisms almost unchanged into evolutionary biology".

An additional difficulty for me was that neither an electronic version of the text nor of any of the illustrations could be found following Dr. Haffer's death, entailing a major reconstruction effort. Only Hans Hudde's tables of species names were in an electronic form. With the generous permission of Herr Hudde, I had to be counted as a co-author only because of the number of contributions that I had to undertake, including re-photographing almost all of the illustrations. I also wrote the Abstract and compiled the reference list.

A further consequence of Dr. Haffer's sudden death was that he was unable to bring his material up to date. He did make new insertions in the main text right up until early 2010, but the citations in those sections based on his earlier works are beginning to show their age and many will have been superseded in recent years. To update these passages would have entailed an immense amount of work, so I have confined my additions to citations of newer important standard publications (handbooks, seminal works on genetics and other new fields, etc.), or of titles which I felt Dr. Haffer would have inserted had their absence been drawn to his attention. Other insertions or remarks by me in the text are in bold placed inside square brackets. Since the work was originally in German, occasional reference is made to a translation of a publication that was originally in English. I have left these citations untouched, although in general the original will also be in the reference list.

This indeed, and not the translation itself, has been the main problem in the preparation of this text for publication. I feel that it is not acceptable for me as translator to add any new material to Dr. Haffer's text, nor indeed to delete anything substantial, when he is no longer present to approve or disapprove. The contribution of his trusted colleague Hans Hudde was restricted to the online Appendices 1–3. I have received many useful remarks and suggestions from anonymous referees, but I hope they will appreciate that for the above reasons I think it would be inappropriate for me to make substantial alterations.

Having said that, the impressive number of considered suggestions and corrections I received from Professor Walter J. Bock of Columbia University deserves special mention. He has gone to great lengths not only in reading my translation most thoroughly – even to the extent of correcting typos and other small errors – but also in providing me with quite a few pages of valuable comment. Now that Jürgen Haffer and Ernst Mayr are no longer with us, Dr. Bock is probably the leading authority on the history of ornithology, including the German material, and so his words carry great weight. Therefore rather than altering the text that was given to me, or introducing comments from a third party, I will set out in this Preface the points made by Dr. Bock.

Walter Bock and Jürgen Haffer were old friends and occasional collaborators, but since they were both active in the same field it was only natural that they did not agree with each other all of the time. The facts of history – names, dates, ideas – are not disputed, but the importance of ideas and theories for future developments can be argued about, and not unreasonably Dr. Bock begs to differ with some of Jürgen Haffer's interpretations as set out here. For example, regarding Chapter 8, "The Stresemann Era", Professor Bock feels that the influence of Erwin Stresemann in North America as described there is somewhat exaggerated. He believes that the New Avian Biology was well under way in the United States by the time Stresemann's work began to have any influence. One reason for this, he asserts, was the less authoritarian structure of the universities outside Germany, as well as the lack of the rigid division between museum and university that hindered career moves in Germany.

Stresemann's *Aves* was little read outside of Central Europe. More than two-thirds of the 2200 printed copies were in fact destroyed in a warehouse fire at the end of the war so its physical distribution and influence were necessarily limited. In addition, German research, both in fact and in reputation, was set back at least a decade by the catastrophe of the Second World War. Without the great proselytizing energy of Ernst Mayr in the U.S., history might have taken a slightly different turn. The influence of Joseph Grinnell (1877–1939) at the University of California, Berkeley in moving ornithology in the same direction as Stresemann, whom he greatly admired, was considerable but restricted to the academy. His ideas were scattered in papers throughout the scientific literature so reached a limited number of people. His successor Alden Miller (1906–1965) had perhaps the greater impact, sending a couple dozen PhD graduates out into the world to take up successful careers in American ornithology. See also Bock (2001).

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Dr. Bock had much to say on the text as a whole. For example, he feels that Dr. Haffer did not sufficiently stress the modernizing role played by Professor Alfred Newton in the UK at the end of the 19th century. However, although Newton was a great ornithologist, and his *Dictionary of Birds* (1893–1896) a masterly compendium of everything that was then known in avian science, and despite the fact that he was one of the first to immediately recognize the revolutionary power of the theory of evolution by natural selection of Darwin and Wallace, he was a life-long conservative with little to no interest in field or laboratory studies. See especially Birkhead & Gallivan (2012).

Despite the incorporation of older material, this book is a genuine addition to Jürgen Haffer's work in that it brings together a longer time-span and – with the inclusion of developments in 20th-century Great Britain – a broader geographical scope than his previous articles. A fascinating novelty is how the development of species knowledge is reflected in the gradual increase in the number of species named. This is made beautifully clear in the three online appendices of names compiled by his friend and collaborator of many years, Hans Hudde. These tables, whose wealth of German vernacular names through the centuries will be a great help to researchers, represent a labor of love by Hans Hudde and an admirable achievement for a man of his advanced years. The slow refining of species recognition and identification is also made clear in the many illustrations accompanying the text. A further aspect of species knowledge that was close to Dr. Haffer's heart was to bring to the attention of the wider ornithological public J.A. Naumann's first book *Der Vogelsteller* [*The Bird-Trapper*] of 1789. The elder Naumann's encyclopedic knowledge of birds is well illustrated by the lengthy extracts from this fascinating work.

For their help in a great variety of ways I would like to express my gratitude to Dr. Karl Schulze-Hagen (Mönchengladbach), Dr. Karl-Ludwig Schuchmann (Zoologisches Forschungsmuseum Alexander Koenig, Bonn), Dr. Eberhard Mey (Thüringer Landesmuseum Heidecksburg, Rudolstadt), Dr. Sylke Frahnert, Dr. Matthias Glaubrecht, and Pascal Eckhoff (Museum für Naturkunde, Berlin), Hans Hudde (Essen), and naturally to my wife Northild Hillcoat-Kayser, who checked my translation most assiduously. I would also like to thank the anonymous referees for their constructive suggestions, but in particular Professor Walter J. Bock for the trouble he took with his very detailed comments. My deepest thanks go to Frau Maria Haffer and Frau Amelie Haffer-Penther for their generous support and encouragement, but above all for their patience.

Brian Hillcoat Berlin, June 2013

INTRODUCTION

The beginnings of ornithology in Central Europe lie many centuries in the past (Fig. 1). Despite this, some ornithologists, who around 1800 and early in the 19th century had published multi-volume handbooks on the birds of Germany, were celebrated in the 20th century as the "founders", "creators", or "fathers" of German-language ornithology, while by comparison the various achievements of their important forerunners were ignored. Here we wish to discuss the work of these early ornithologists in Europe, especially in the period from the 16th to the 18th century, when the foundations of European ornithology were laid. Until now, the wealth of information on bird species accumulated by ornithologists of this era has never been presented in a tabular form or reviewed using comparative methods.

Zoologists and botanists began using Linnaean nomenclature – in which every species is accorded a Latin-based generic name and specific name – in the second half of the 18th century. Thus every animal and plant species had a unique binomial "label". At this time almost all of these organisms had long possessed one or more German vernacular names, so the new Latin names for bird species in the German-speaking areas denoted creatures that were already familiar to people.

We wish to pursue several aims in this work:

(1) To identify, by using several correlation tables, the German bird names employed in the writings of early ornithologists that are no longer current, in order to facilitate the study of the original texts;
(2) To document the often impressive biological and field-ornithological knowledge about Central European birds that existed in the period 1500–1900. It is not our intention to trace the development of faunistic expertise regarding the geographical distribution of birds in Central Europe;
(3) To illustrate the steady increase in the number of known species in Central Europe over the last few centuries;
(4) To show how Central European field ornithology flourished in the 18th century. To do this most effectively we will review in detail the contents of important publications from that time which today are almost forgotten or are extremely difficult to find in the original. Works such as Ray (1691, 1717), von Göchhausen (1710), Frisch (1733–1763), and J.A. Naumann (1789) will be discussed, with many passages being quoted in full;
(5) To encourage greater interest in the ornithological thinking of these early masters, rather than concentrating on biographical details.

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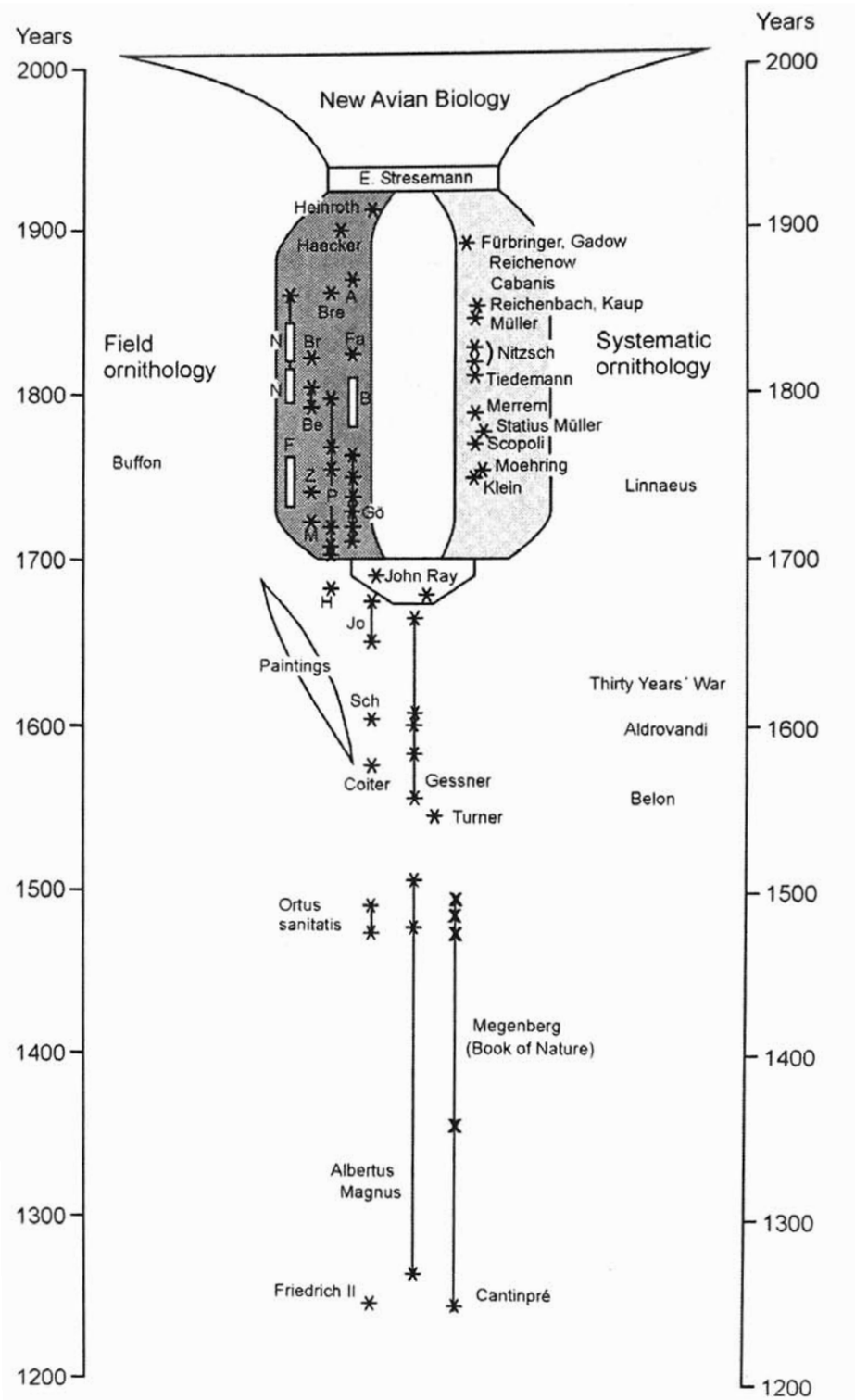

Fig. 1. The development of ornithology in Central Europe 1200–2000. Asterisks and open bars denote significant publications. The word "Paintings" indicates the existence of several collections of bird paintings. Abbreviations are: Sch – Schwenkfeld, Jo – Johnston, H – Hohfeld, M – Marsili, P – Pernau, Gö – Göchhausen, Z – Zorn, F – Frisch, Be – Bechstein, B – Buffon (German translation), N – Naumann, Bre – C.L. Brehm, Fa – Faber, Br – A.E. Brehm, A – Altum. There is no horizontal scale (slightly altered from Haffer 2007a).

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During the 19th and into the early 20th century, ornithology in Central Europe was deeply divided into systematic ornithology and field ornithology (the natural history of birds). In Berlin during the early 1920s, Erwin Stresemann (1889–1972) initiated the integration of both branches into a unified *New Avian Biology* (Haffer 2001, 2007a; Birkhead 2008; Birkhead & Charmantier 2009). Other global histories of ornithology have neglected to discuss these crucially important developments in Central Europe (e.g. Farber 1982; Walters 2003; Chansigaud 2009).

The roots of the scientific study of birds in Central Europe lay in the various activities of people interested in animals and specifically birds, like hunting, trapping, collecting, the keeping of birds in captivity, or simply taking aesthetic pleasure in the beauty of birds. It was an important step towards a scientific attitude if an author also showed an interest in species that were of significance neither for the kitchen nor for the cage. Bird collections have existed since the early 16th century; they consisted of mounted or mummified specimens whose durability, however, was poor until the employment of arsenic as protection against invertebrate pests from around the mid-17th century (Schulze-Hagen et al. 2003). Some early authors were primarily motivated by the medical uses of birds. Among these people with an early interest in the avian world were emperors and princes, counts, generals, clergymen, artists, teachers, and many other people.

Brief biographies of almost all the ornithologists mentioned here have been published by Gebhardt (1964, with details of additional literature) and can be read there. Therefore in this paper we will not go into biographical details of the early ornithologists, but will instead concentrate on the results of their work.

Ornithology from the 16th to the 19th century

As early as the Middle Ages, the Hohenstaufen Emperor Friedrich II, in the general ornithological chapter of his handbook on falconry (*De arte venandi cum avibus*, before 1248), made remarks on the life histories of about 100 bird species (Henss 1970; Kinzelbach 2008). Around the same time, the Dominican friar Albertus Magnus dealt with a similar number of species (Balss 1928), an account that underpinned the basic learning of the early ornithologists. If one wanted a strict definition of who the "father" of Central European ornithology was then Friedrich II and Albertus Magnus would have to be called its "fathers". Those ornithologists who were prominent in later centuries were variously called "old masters", "pioneers", or "trailblazers" who, through their works, ensured important advances in the science (Stresemann 1951; Haffer 2006, 2007a).

While nature in earlier times was simply understood to be a manifestation of the Mind of God, after the 15th century researchers themselves increasingly studied natural objects.

(1) In the 16th century several naturalists collated their knowledge in different fields to create comprehensive encyclopedias; important among them was Conrad Gessner in Zürich (see online Appendix 1).
(2) In the 17th century we see the *beginnings* of field ornithology, when Caspar Schwenckfeld (1603) and John Jonston (1650) published their surveys of birds, while Ray (1676, 1678) along with Willughby gathered together the results of their studies in England and Central Europe in a first handbook of ornithology.
(3) The *foundations* of field ornithology were laid down in the first half of the 18th century, with the outstanding research work of four men working independently of each other in northern, central, and southern Germany: A. von Pernau in Sulzbach near Coburg (Franken), H.F. von Göchhausen in Sachsen-Weimar (Thüringen), J.L. Frisch in Berlin and Brandenburg, and J.H. Zorn in Pappenheim, Sachsen-Coburg (Franken). (online Appendix 2).
(4) In the following four decades (1750–1788) hardly any progress was made in field studies (Stresemann 1941a). Nevertheless, translations of work from other languages appeared, such as Statius Müller (1773), Buffon (1772–1809), Pennant (1787), and the overviews compiled by Klein (1750, 1760) and Halle (1760).
(5) The *flourishing* of field ornithology in the late 18th and early 19th centuries is typified by the work of Johann Andreas Naumann (1789), J.M. Bechstein (1791–1795), and Johann Andreas Naumann & Johann Friedrich Naumann (1795–1817). (online Appendix 3).
(6) This period was followed by the blossoming of field ornithology, its "Golden Age", when J.F. Naumann (1820–1844, 1860), C.L. Brehm (1820–1822, 1823–1824, 1831), F. Faber (1824–1827, 1825–1826), and C. Gloger (1834a,b) were active in Central Europe and published their great works. See Fig. 2.

(1.) Renaissance ornithologists: 16th century

The Renaissance period of the 15th and 16th centuries is characterized by the discovery and re-appropriation of Classical learning following the era of the "dark" Middle Ages. The starting point for natural "scientists" were the zoological, botanical, and mineralogical writings of Aristotle, Theophrastus, and Dioscorides (Bäumer 1991). This knowledge was supplemented in the zoological works of the encyclopedists Gessner around 1550 and Aldrovandi around 1600 by their own observations, as well as those of their contemporaries, resulting in an all-encompassing picture. The endeavors of these decades also led to the emergence of specialized fields, such as comparative

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anatomy, physiology, ornithology, ichthyology, and entomology. The first works devoted solely to birds were those by G. Longolius of Cologne (1544), the Englishman W. Turner (1544), and the Frenchman P. Belon (1555), all of whom were principally interested in identifying the species mentioned in Classical literature. Nevertheless, these authors did include their own observations in their writing, while Belon in particular also used good illustrations, which were absent from the books of his two colleagues. The popular books written in German on plants and animals by Adam Lonitzer (*Kreuterbuch*, 1557) [*Herbal*] and Jacob Horst (*Von den wunderbarlichen Geheimnissen der Natur*, 1579) [*The wonderful secrets of nature*] also contain descriptions of animals, including birds, and were reprinted many times over the next hundred years.

For these authors and their readers all living things were holy, since they had been created by God. To occupy oneself with them could therefore lead to a deeper understanding of the Creator. The beauty of nature led to God through the contemplation of His works. This philosophy in German learning of the 16th and 17th centuries (Crowther-Heyck 2003) prepared the ground for the rapid spread of physico- or natural theology in the German-speaking regions at the beginning of the 18th century.

Hans Sachs – Poet of the Reformation (1531). Hans Sachs (1494–1576) was the most important poet of the Reformation. He lived in Nürnberg, working initially as a master shoemaker but later becoming committed to the ideas of the Reformation and to Martin Luther, as expressed in his aphoristic verses on the "Wittenberg Nightingale" (Goetze 1890). Sachs and his witty aphorisms rapidly became famous in Germany as he published further poems in dialogue form supporting the aims and dissemination of the Reformation. In his poetry he also wrote of his home town Nürnberg, composed farces, Shrovetide plays, comedies, rhyming explanations of woodcuts, and also vehemently attacked the scourges of highway robbery and murder. In the 16th century Sachs was influential in many areas of cultural life. His poem

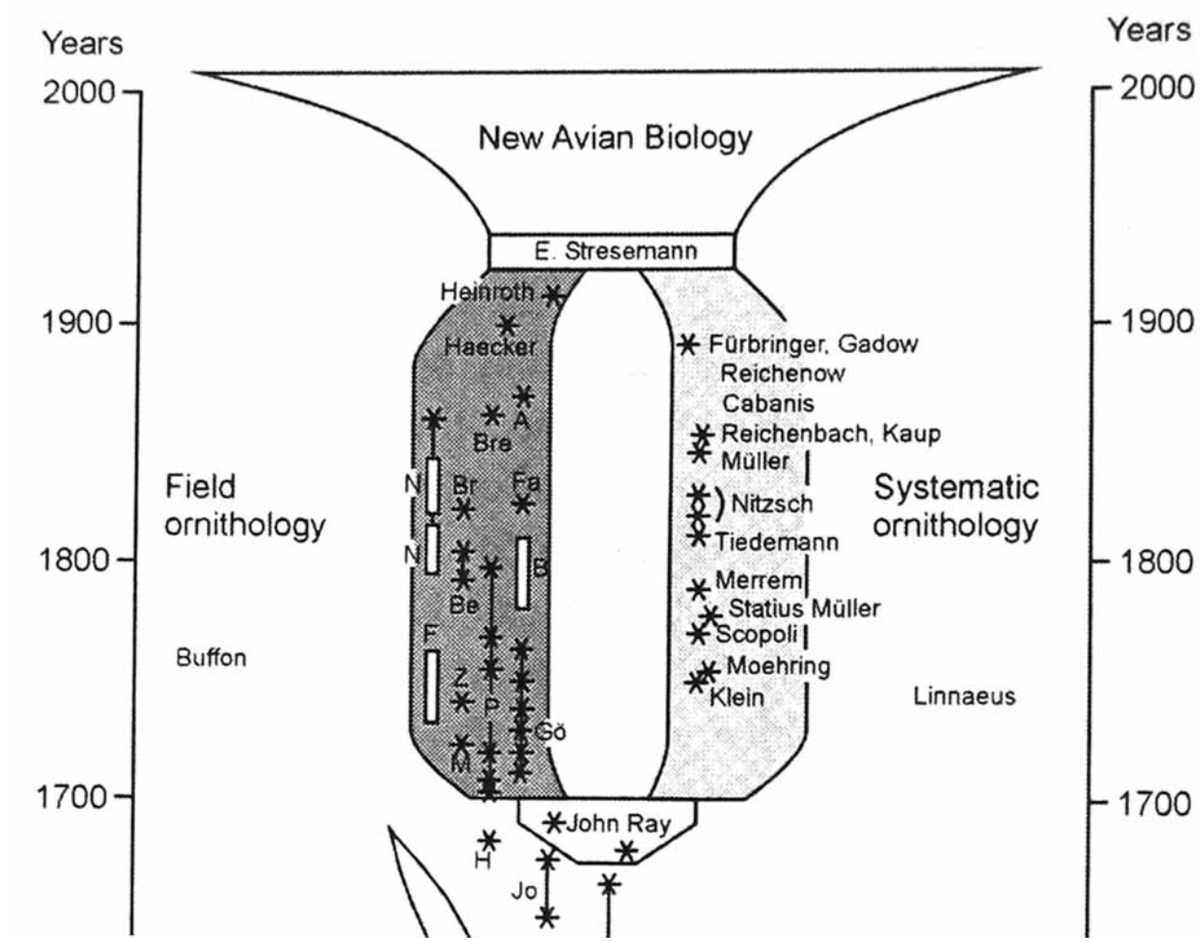

Fig. 2. The development of ornithology in Central Europe 1700–2000 (detail from Fig. 1).

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of 1531, *Das Regiment der anderthalb hundert Vögel* [*The regiment of one-and-a-half hundred birds*], reproduced by Suolahti (1909: 462–472), provides a good overview of the vernacular names of birds common in the Nürnberg area. According to our count, 107 species are referred to (online Appendix 1) which we have correlated with their modern names using Suolahti (1909). What is missing in the poem is any mention of ducks or wetland birds, for which there must have been many names in southern Germany, and only a few raptors appear in the work.

Early writings on European birds – Longolius and Turner. Gilbertus Longolius (1507–1543) was the first Renaissance zoologist to publish an exclusively ornithological book (Bäumer 1991; Kinzelbach 2012). The manuscript, published in 1544 after his death by his friend William Turner in Cologne, was in the form of a dialogue, a very popular literary genre at the time. Longolius discusses with his opposite number Pamphilus the names or identity of the birds described in Classical literature. The birds dealt with are Peacock, Jay, Pheasant, Capercaillie, Hazel Grouse, Black Grouse, Red-legged Partridge, Guineafowl, Quail, snipe or godwit, plover, thrush, lark, sparrow, and pigeons. The Red-legged Partridge is mentioned as occurring in the central Rhine Valley near Landskron Castle (lower Ahr Valley), not far from Remagen, where this species has not been recorded for hundreds of years. The death of the author prevented a continuation of the work.

William Turner (1508–1568), being a non-conforming Protestant, was several times forced to flee from England for religious and political reasons, and lived for many years in Cologne (Kinzelbach 2012). Here his book *Aves praecipuarum*, on the identity of birds in the works of Aristotle and Pliny the Elder, appeared in 1544. His commentaries on the individual species are based on his own observations, for instance the account of the Great Grey Shrike (*Lanius excubitor*) quoted by Stresemann (1951: 14–15). A new ornithological science begins with Turner. He treated the following species:

Goshawk, Kingfisher, Mallard, geese, eagle, heron, Goldfinch, Hazel Grouse, *Sylvia* warbler, Eagle Owl, Nightjar, Blue Rock Thrush, White Stork, Hawfinch, pigeons, Quail, Carrion Crow, Raven, Pied/Grey Wagtail, Cuckoo, Black-winged Stilt, Shelduck, Blackcap, Chaffinch, Brambling, Yellow Wagtail, Coot, terns, Sky Lark, domestic chickens, Woodcock, Jackdaw, Crane, martins/swallows, Ptarmigan, Greenfinch, Redpoll/Siskin, Nightingale, gulls, Bee-eater, Blackbird, harrier, Great Grey Shrike, Bearded Vulture, owl, swan, Corn Crake, Barn Owl, tit, plover, sparrow, Peacock, Grey Partridge, Pheasant, Phoenix, Magpie, woodpecker, parrot, pelican, Purple Gallinule, Wren, Robin, Common Redstart, Nuthatch, Black Grouse, Goldcrest/Firecrest, Moorhen, thrush, Hoopoe, and vulture.

The encyclopedist Conrad Gessner[1] – a Pliny of the Renaissance. In Zürich, after the fashion of the Roman Pliny the Elder, the universal scholar Conrad Gessner (1516–1565) (Fig. 3) wrote a four-volume *Naturgeschichte der Tiere* [*Natural history of animals*], an encyclopedic work of reference ("thesaurus" or "pandect") that was designed to replace an entire library (Bäumer 1991). For this he requested information from friends in several European countries, stressing that his *Historia animalium* would contribute to the glorification of the works of God, whose craftsmanship could especially be discerned in the very smallest animals, like the ants. The species are ordered alphabetically, though with certain divergences from the system in the raptors and game-birds, where species that are obviously closely related are placed together. The avian volume appeared in 1555 (*Historiae animalium liber III: De Avium Natura*). Gessner described many species for the first time and introduced the Latinized form of their names into science. Two hundred years later Linnaeus took over most of Gessner's Latin nomenclature, which is why many are still in use today, or until very recently (e.g. *Parus cristatus*, *P. ater*, *P. palustris*, *P. major*). Gessner named as forerunners of his bird book those of Longolius and Turner (see above). He had heard of the ornithological publication by the Frenchman Pierre Belon (1555) but had not been able to see a copy, he wrote.

Das Vogelbuoch (1557) [*The book of birds*] is a shortened German translation in 526 pages of Gessner's bird volume of 1555 (779 pages). Since this book was intended as a popular compendium appealing to the broadest possible audience, all of the philological embellishment and mythical creatures were left out.

In his great encyclopedia *Ornithologia* (1599–1603), the Italian Ulisse Aldrovandi deliberately turned away from the idea of listing species alphabetically, using systematic (including anatomical) concepts to arrive at a "natural" order so that related species would not be artificially separated from each other. His work is more voluminous than Gessner's.

Gessner described 182 bird forms fairly precisely, so that they can be more or less identified today (Ziswiler 1969); see Figs. 4a–d. Occasionally he classed birds in male and female or juvenile and adult plumages as belonging to different species. The most difficult identifications are those of ducks, geese, seabirds, and waders, since Gessner had very little personal experience of them. On the other hand, those species that are accurately described (apart from the very common ones like chickadees (tits), etc.) are the Alpine birds Wallcreeper, Alpine Accentor, Citril Finch, Snow Sparrow, Nutcracker, as well as many others, including Serin, Waxwing, Stone-curlew, and Water Rail. The Waldrapp, which still bred in Switzerland in Gessner's day, can be identified as today's Bald Ibis (*Geronticus eremita*), now completely extirpated in Europe. Ziswiler (1969) created a synoptic table of Gessner's bird names,

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Fig. 3. Portrait of Conrad Gessner (from Stresemann 1951; Bildarchiv des Museums für Naturkunde, Berlin).

which we have used to compile the list in online Appendix 1.

Springer & Kinzelbach (2009) have treated Gessner as a "scientist" of the early modern era and have collated a total of 241 bird species from his books, the most important collection of avifaunistic data from 16th-century Central Europe.

Numerous bird illustrations by Gessner (1555), Belon (1555), Cyganski (1585), Aldrovandi (1599–1603), and in the *Thesaurus Picturarum* of Marcus zum Lamm (1577–1606; see Kinzelbach & Hölzinger 2000) were made using preserved birds as models. In Gessner (1555) in particular, the great majority of the illustrations are of mounted or mummified specimens (Schulze-Hagen et al. 2003).

Mateusz Cyganski published a popular handbook in 1585 on game-birds. Over 150 species are mentioned and 79 of them depicted in simple woodcuts (Nowak 1985). The Protestant theologian Johannes Wigand (1586) wrote about the Common Cuckoo, observed European Nightjars on the nest, listened to the drumming of the Common Snipe, and described some details from the life of the Eagle Owl (Hildebrandt 1930).

(2.) The beginnings of field ornithology: 17th century

The first extensive local avifauna (for Silesia) in Europe was published at the beginning of the 17th century (Schwenckfeld 1603), and also at this time several naturalists were collecting color illustrations of Central European birds, but these were never published, or only as selections centuries later (Hackethal 1992, 2001; Haffer 2007a). See especially Mey & Hackethal (2012).

Marcus zum Lamm was a Protestant cleric in Heidelberg, where from 1570 onwards he collected three volumes of watercolor paintings of birds from the general region of the upper Rhine Valley, consisting of 207 species, of which 60 are exotic species from abroad (see online Appendix 1). These pictures cover the time span of the climate change around 1580, when the "Little Ice Age" began. Marcus zum Lamm recognized the causal relationships between this climatic change and the disappearance of several "Mediterranean" bird species from the Rhine Valley (Fig. 5) (Lauterborn's Theory). Kinzelbach (1995a,b,c, 1998, 2004), Kinzelbach & Springer (1999), and Kinzelbach & Hölzinger (2000) trace invasions into Central Europe of Bohemian Waxwing (*Bombycilla garrulus*), Common Rosefinch (*Carpodacus erythrinus*), Common Redpoll (*Carduelis flammea*), and European Serin (*Serinus serinus*). See online Appendix 1.

The Thirty Years' War (1618–1648) between Catholic and Protestant rulers ravaged Central Europe, and it was to be many decades before countries recuperated from the catastrophe. No real progress in natural history research, including of course ornithology, was made during that century in the region. Aitinger's report on bird-trapping (1626–1631) contains some biological information regarding birds, but the author himself was killed in the chaos of the war. The text of John Jonston's *Historia naturalis* (1650–1653) was compiled from the handbooks of Gessner and Aldrovandi and contained barely any new information, but because it included many plates with simplified illustrations it was widely read, thus contributing to a new interest in the natural world after the horrors of war, as did the last edition of Gessner's *Vogelbuoch* in 1669.

A new dawn in natural history studies, and in ornithology in particular, rose with the work of the English naturalist John Ray (1627–1705), who, together with his young friend and co-worker Francis Willughby (1635–1672), published a survey of all bird species known at the end of the 17th century (Ray 1676, 1678). These books represented a foundation on which the systematic ornithology of the following centuries could be built. This seminal work was studied throughout the whole of Europe, which is why Willughby and Ray's list of European bird species is included here. Ray was the first biologist to introduce the concept of successful sexual reproduction as a criterion for defining a species. Concerning plants, he wrote: "One species never springs from the seed of an-

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a

b

c

d

Figs 4a–d. Four plates from Gessner (1582 edition). 4a: Great Crested Grebe; 4b: Eurasian Eagle Owl; 4c: Western Capercaillie; 4d: Snow Bunting (top), Rock Bunting.

other nor vice versa." Species are reproductive communities that have existed unchanged since the Creation. As a first account of biological research on flora and fauna using field studies, Ray's book *The Wisdom of God manifested in the Works of the Creation* (1691) is of special importance. It went into 13 editions and was translated into French and German: *Gloria Dei oder Spiegel der Weißheit und Allmacht Gottes: offenbahret in denen Wercken der Erschaffung* (1717). In this publication, Ray examines the problems of form and function in birds (and other animals) as well as their adaptation to their environment, discusses the skill with which birds build their nests (differently depending on species), points out their lightweight and hollow bones and their system of air sacs, and describes details of feather structure and the function of the preen gland. Physiological aspects of this kind need to be studied by scientists, Ray stressed.

A first local naturalist – Caspar Schwenckfeld (1603). Schwenckfeld was a pious Protestant, strict believer in the literal truth of the Bible, doctor, and naturalist, in particular a botanist (student of Bauhin in Basle and Gessner in Zürich), and lived in Silesia from 1563 to 1609. He was the town physician, an official post, firstly in Hirschberg and at the end of his life in Görlitz. In his free time he explored, in the course of many long walks, the world of plants and animals in the high hills of the Riesengebirge (Karkonoski in Polish, Krkonoše in Czech), also collecting fossils and minerals. In 1600 his *Stirpium et fossilium Silesiae Catalogus* (407 pages) was published in Leipzig, the very first scientific description of nature in Silesia, containing the first floristic and paleontological study of the region. The plants are listed alphabetically according to their Latin names. His most important work appeared in 1603 in Bratislava, a fauna of Silesia with the

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Fig. 5. Male Red-legged Partridge (Marcus zum Lamm; from Kinzelbach & Hölzinger 2000).

title *Therio-tropheum Silesiae* (563 pages), the "Silesian zoological garden", dealing with the mammals, reptiles, birds, fish, and insects of his homeland – the first local fauna known anywhere in the world, in which animals are separated according to where they live, their way of life, and how they organize themselves. In 1607 he published a further work, a monograph in German on the spa at Warmbrunn in Silesia (Cohn 1888; Gebhardt 1964).

Of the 154 native birds known to him (online Appendix 1), he described the voice, food, distribution, nest, number and color of the eggs. The species are in alphabetical order, are not illustrated, and are arranged according to the following scheme: name (Latin, Greek, German), brief description, remarks on reproduction and usefulness. The book is a lexicon for reference purposes, in which some exotic animals also appear (e.g. elephant, leopard, guinea pig, monkeys, parrot, ostrich). All the species had already been mentioned in the contemporary works of Gessner, Aldrovandi, Wotton, Belon, and Rondelet. Schwenckfeld probably took many species and the broad systematics from these authors. He described no new bird species, while some mythical animals like unicorn and phoenix were apparently regarded by him as real. For the compilation of the Central European bird species known to Schwenckfeld we used a copy of his book in the Martin Opitz Library in Herne.

The opinion widely held in his time that "no organism is so small that it does not radiate something of the divine" (Bäumer 1996: 186) was also stressed by Schwenckfeld. Outstanding men of God, mighty kings, and the cleverest doctors had all investigated the world of nature in order to praise the Creator. Knowledge of nature leads to knowledge of God was the prevailing philosophy within which the naturalists pursued their studies.

A compiler – John (Jan or Johannes) Jonston (1650). He was a Polish doctor, naturalist, and polymath of Scottish extraction (Fig. 6). Following the end of the Thirty Years' War (1648), his *Historia Naturalis Animalium* (with 248 plates and almost 3000 illustrations from the workshop of the Merian family in Frankfurt a. M.) promoted the new and growing study of the animal world. The volume covering the birds was published in 1650 (Fig. 7). They are divided, as was usual at the time, into landbirds (birds of prey, insect-eaters, seed-eaters) and waterbirds (with webbed or unwebbed feet). Their method of feeding is the most important characteristic. Book 1 deals with the birds of prey, Book 2 with the plant-eaters (seed- and berry-eaters), Book 3 with the insect-eaters (songbirds and non-songbirds), Book 4 with the web-footed waterbirds (meat-, insect- and vegetation-eaters). In Book 6 "exotic birds" are presented, with an appendix on mythical birds such as griffin or phoenix.

According to Bäumer (1991), "the book on birds is in general a readable abridgement of the corresponding volume of Aldrovandi (1599–1603), although supplemented by quotes from Gessner and contemporary descriptions of birds from America, especially Brazil. By its appealing style and restriction to basic scientific details, the impression given by Jonston's treatment of birds is that it is almost like a forerunner of today's biological field-guides" (p. 139), and "by being limited to natural history facts, fleshed out by a few references to the medicinal uses of some species, a practical compendium of animals was produced, illustrated for the first time by copperplate engravings" (p. 149), which were in the main taken from Aldrovandi and Gessner (Fig. 8). Jonston's compendium was published in many editions in Latin, German, English, Dutch, and French, and hence was very widely read. Jonston did not include any observations of his own in the text, which was purely a compilation, the main reason why Stresemann's (1951: 24) later judgement was so devastating: "The worst animal books have always found the most purchasers!".

Jonston's scholarship extended to many spheres of learning, and he spoke 12 languages. He published writings on medicine, pharmacology, botany, zoology, and history, and his great desire was to produce textbooks with the aim of disseminating general knowledge. In this he always focused on the animal itself, leaving all semantic and emblematic aspects to one side. In the spirit of the later physi-

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Fig. 6. Portrait of John Jonston (from Miller 2008).

Fig. 7. Title page of Jonston (1650).

co-theologians, he recommended that his readers concern themselves with natural phenomena because this encouraged the adoration of the power and goodness of the Almighty. Further publications on the character of Jonston's work are those of Matuszenski (1989) and Miller (2008).

Ornithologists in England – Francis Willughby and John Ray (1676, 1678). Early ornithlogists classified birds in an ecological fashion, on the basis of their preferred habitats (water, fields, woodland), without finding satisfactory solutions to the problem of how to categorize birds in groups. In their important work *Ornithologiae Libri Tres*, which initially appeared in Latin (1676) (Fig. 9) and then in English (*The Ornithology of Francis Willughby*, 1678) (Fig. 10), Willughby and Ray separated birds into units that often agree with modern groupings. For their classification they used the form of birds: bill shape, foot structure, and body size, similar to Linnaeus in the 18th century. This system was Ray's idea, while Willughby collected numerous notes on individual species during their joint travels in England and in western and Central Europe. See online Appendix 1.

In the years 1663 to 1666 Willughby and Ray journeyed through Holland and the lower Rhine region, followed the Rhine Valley to Strasbourg, and then traveled eastwards

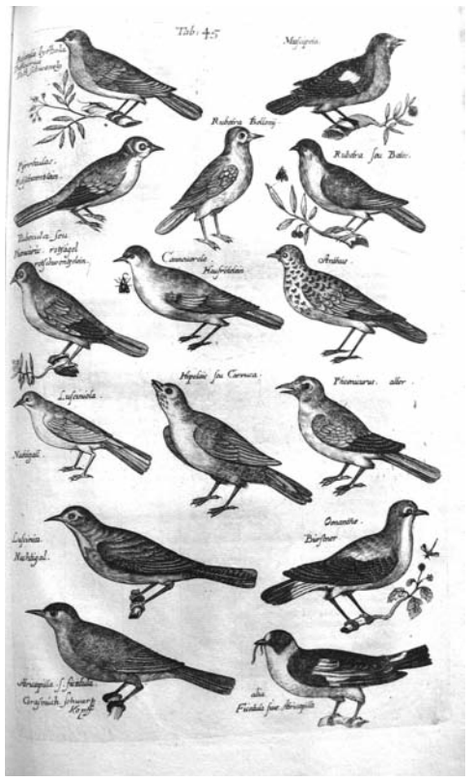

Fig. 8. Plate from Jonston (1650) with various flycatchers, thrushes, and warblers.

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to Vienna from where they moved south to Italy. In their textbook, *Ornithology*, many records of species that they found on markets in Germany and Italy can be found. In addition, they purchased color illustrations in Strasbourg, Nürnberg and other cities (Charmantier & Birkhead 2008). In this ornithological handbook, which was largely conceived by Ray, they described every species so exactly that they can be easily recognized, and repeat descriptions of male and female or juvenile and adult were avoided. Ray was dissatisfied with the quality of the illustrations, although he still regarded them as better than other contemporary copperplate engravings of birds (Figs. 11a, b). The plates are black and white, though at least one copy exists with hand-colored plates, in the library of the famous diarist Samuel Pepys (Montgomerie & Birkhead 2009). Here, the colors of most of the depictions are good, and the species easily identifiable, though the toucan on Plate 20 ("Pica Brasiliensis Toucan") resembles no existing bird, appearing to be a conglomeration of several species. Raven (1942, 1950) provides a clear and detailed description of Ray's work.

Many 17th-century theological scholars believed that the study of nature could not be approved of for Christians: nature represents a temptation leading away from the path to redemption and salvation for mankind. John Ray in Cambridge preached the reverse: that the study of plants and animals is pleasing to God, revealing his plan in the Creation. At the age of 60, Ray brought his sermons and the results of his decades of nature study together in his most popular book, written in English rather than the Latin of his other works, which appeared in London in 1691: *The Wisdom of God manifested in the Works of the Creation* (Fig. 12). The German translation of 1717 carried the title *Gloria Dei oder Spiegel der Weißheit und Allmacht Gottes: offenbahret in denen Wercken der Erschaffung*. In this book, Ray sets out his concept of natural or physico-theology, in which living organisms are in a miraculous way adapted to their environment and hence are suitable objects of study, with the aim of praising God and recognizing the plan of the Creator. By stressing the significance of form and function, with his extensive works on plants, birds, mammals, fish, and insects between 1676 and 1713, Ray laid the intellectual foundations for the ornithologists, entomologists, and other specialists in 18th-century Europe. He encouraged naturalists to closely observe plants and animals in their natural habitats in order to celebrate the wisdom of the Creator of the world. He saw the order of the universe, the life of plants and animals, and the functioning of nature as a manifestation of the Holy Spirit (Raven 1942).

What was new in *The Wisdom of God* was that Ray moved from the simple tasks of a naturalist (identification, description, classification) to an interpretation of the biological significance of structural characters and physiological processes, and an investigation of the adaptations of organisms to their environment, their behavior and in-

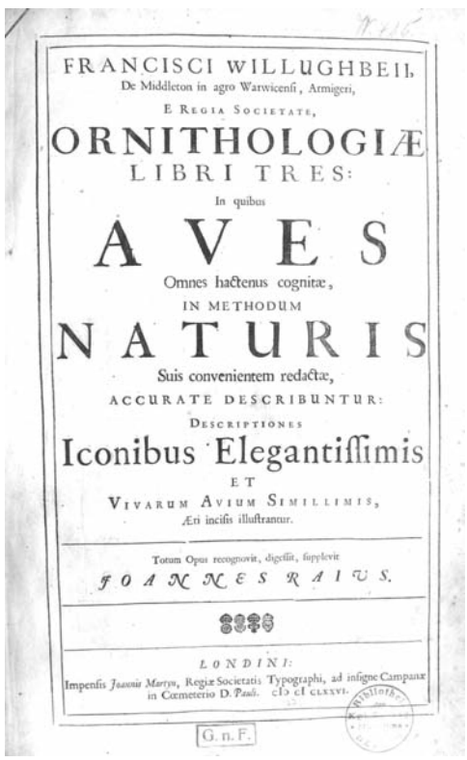
FRANCISCI WILLUGHBEII,
De Middleton in agro Warwicensi, Armigeri,
E Regia Societate,
ORNITHOLOGIÆ
LIBRI TRES:
In quibus
AVES
Omnes hactenus cognitæ,
IN METHODUM
NATURIS
Suis convenientem redactæ,
ACCURATE DESCRIBUNTUR:
Descriptiones
Iconibus Elegantissimis
ET
Vivarum Avium Simillimis,
Æri incisis illustrantur.
Totum Opus recognovit, digessit, supplevit
JOANNES RAIUS.
LONDINI:
Impensis Joannis Martyn, Regiæ Societatis Typographi, ad insigne Campanæ in Cœmeterio D. Pauli. CIↃ CLXXVI.
G. n. F.

Fig. 9. Title page of Ray (1676).

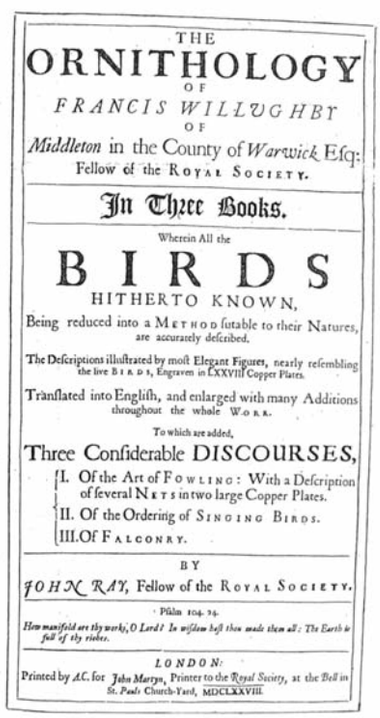
THE
ORNITHOLOGY
OF
FRANCIS WILLUGHBY
OF
Middleton in the County of Warwick Esq:
Fellow of the Royal Society.
In Three Books.
Wherein All the
BIRDS
HITHERTO KNOWN,
Being reduced into a Method suitable to their Natures, are accurately described.
The Descriptions illustrated by most Elegant Figures, nearly resembling the live Birds, Engraven in CXXVIII Copper Plates.
Translated into English, and enlarged with many Additions throughout the whole Work.
To which are added,
Three Considerable DISCOURSES,
I. Of the Art of Fowling: With a Description of several Nets in two large Copper Plates.
II. Of the Ordering of Singing Birds.
III. Of Falconry.
BY
JOHN RAY, Fellow of the Royal Society.
Psalm 104. 24.
How manifold are thy works, O Lord! In wisdom hast thou made them all: The Earth is full of thy riches.
LONDON:
Printed by A.C. for John Martyn, Printer to the Royal Society, at the Bell in St. Pauls Church-Yard, MDCLXXVIII.

Fig. 10. Title page of Ray (1678).

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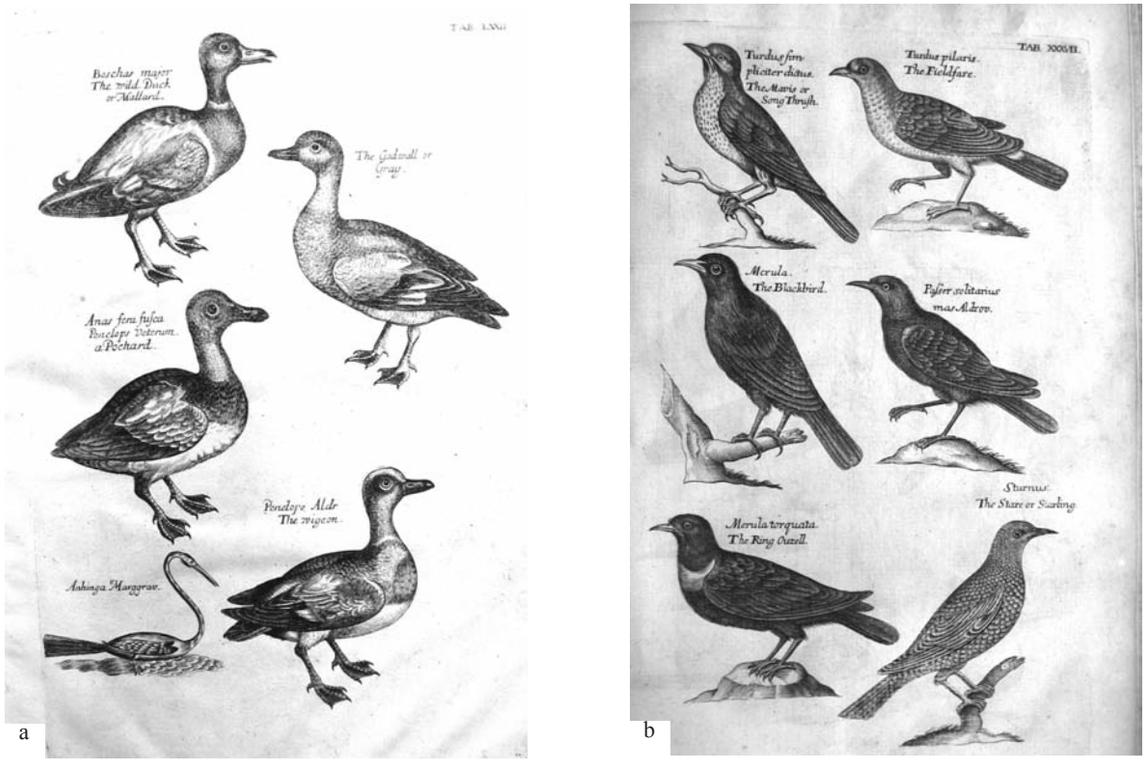

Figs 11a, b. Two plates from Ray (1678). 11a: ducks and *Anhinga* sp.; 11b: thrushes and Common Starling.

stincts (Raven 1942: 452–453). In order to stress the crucial importance of this naturalist to the development of ornithology we feel it appropriate to quote at length from his pioneering work. In the following passages we summarize his most important conclusions relating to birds, using the 1826 edition that was reprinted by the Ray Society in 2005. Key statements are emphasized in italics, while any added comments of ours appear in square brackets.

In the Preface (p. ix) Ray assures the reader that he has "been careful to admit nothing for matter of fact, or experiment, but what is undoubtedly true, lest [he] should build upon a sandy and ruinous foundation; and by the admixture of what is false, render that which is true suspicious", and continues: (1) "The belief of a deity being the foundation of all religion ….. must be demonstrated by arguments drawn from the light of nature and works of creation …….you may hear illiterate persons ……. affirming that they need no proof of the being of a God, for that *every pile of grass, or ear of corn, sufficiently proves that: for … all the men of the world cannot make such a thing as one of these; and if they cannot do it, who can, or did make it but God?* To tell them that it made itself, or sprung up by chance, would be as ridiculous as to tell the greatest philosopher so" (pp. x–xi). (2) This argument here "serves not only to demonstrate the being of a Deity, but also to illustrate some of his principal attributes; as namely, his infinite power and wisdom …….. the sun and moon, and all the heavenly hosts, are effects and proof of his almighty power …… the adapting all the parts of animals to their several uses: the provision that is made for their sustenance" (p. xi). By the "Works of the Creation" of his title, Ray means "*the works created by God at first, and by him conserved to this day in the same state and condition in which they were at first made*". So for Ray there were no changes and no evolution, only the constancy of the universe and all plant and animal species: "Conservation ….. is a continued creation".

"Animate bodies are divided into four great genera or orders, beasts [chiefly quadrupeds, with mammals, reptiles, etc.], birds, fishes, and insects."

"The species of beasts, including also serpents, are not very numerous; of such as are certainly known and described, I dare say not above 150…….I reckon *all dogs to be of one species, they mingling together in generation, and the breed of such mixtures being prolific* [= definition of a species!].

"The number of birds known and described may be near 500 ……..we may suppose the whole sum of beasts and birds to exceed by a third part, and fishes by one half, those known" (p. 24). Regarding the plants, "there are a great many, I might say some hundreds, put down for different

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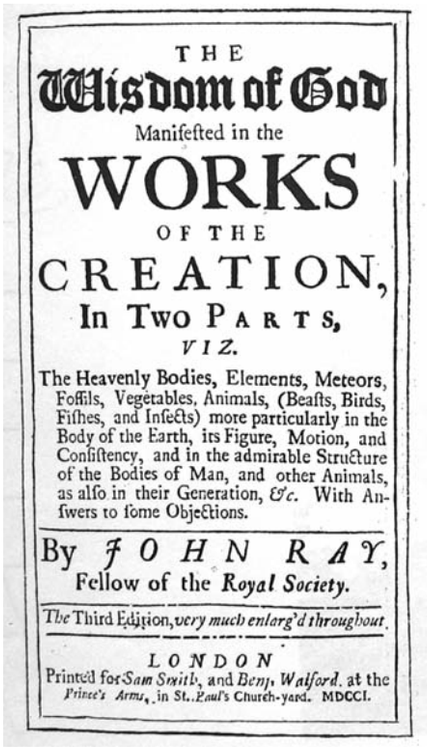
THE
Wisdom of God
Manifested in the
WORKS
OF THE
CREATION,
In Two Parts,
VIZ.
The Heavenly Bodies, Elements, Meteors, Fossils, Vegetables, Animals, (Beasts, Birds, Fishes, and Insects) more particularly in the Body of the Earth, its Figure, Motion, and Consistency, and in the admirable Structure of the Bodies of Man, and other Animals, as also in their Generation, &c. With Answers to some Objections.
By JOHN RAY,
Fellow of the Royal Society.
The Third Edition, very much enlarg'd throughout.
LONDON
Printed for Sam Smith, and Benj. Walford, at the Prince's Arms, in St. Paul's Church-yard. MDCCI.

Fig. 12. Title page of John Ray's *Wisdom of God* ... (1701 edition).

species, which in my opinion *are but accidental varieties*" in respect of their characters, which are not "sufficient to constitute a specific difference" (p. 27).

"If the number of creatures be so exceeding great, how great, nay, immense, must needs be the power and wisdom of him who formed them all!" (p. 27). "God can and doth by different means produce the same effect ….. the various ways of extracting the nutritious juice out of the aliment, in several kinds of creatures. (1) In man and the viviparous quadrupeds, the food moistened with the spittle (saliva) is first chewed and prepared in the mouth, then swallowed into the stomach ……. (2) In birds there is no mastication or comminution of the meat in the mouth; but in such as are not carnivorous, it is immediately swallowed into the crop or craw …….. where it is moistened and mollified by some proper juice ……. And thence transferred into the gizzard or musculous stomach, where ……by the working of the muscles……and by the assistance of small pebbles (which the creature swallows for that purpose) it is, as it were, by millstones ground small, and so transmitted to the guts" (p. 30). "The works of God ….. are all very wisely contrived and adapted to ends both particular and general" (p. 31).

Preservation of species by sexual reproduction. "It is the great design of Providence to maintain and continue every species ….. Why can we imagine all creatures should be made male and female but to this purpose? …… Why in viviparous animals, in the time of gestation, should the nourishment be carried to the embryon in the womb, which at other times goeth not that way? When the young is brought forth how comes all this nourishment then to be transferred from the womb to the breasts or paps ?….. a great proof and instance of the care that is taken, and provision made for the preservation and continuance of the species" (pp. 101–102).

"That ….. birds should all lay eggs, and none bring forth live young, is a manifest argument of divine providence, designing thereby their preservation ……. For if they had been viviparous, the burthen of their womb, if they had brought forth any competent number at a time, had been so great and heavy, that their wings would have failed them, and had become an easy prey to their enemies: or if they had brought but one or two at a time, they would have been troubled all the year long with feeding their young, or bearing them in their womb" (p. 103).

To facilitate the transition of a chick from liquid nourishment in the egg to solid food after hatching "nature hath provided a large yolk in every egg, a great part whereof remaineth after the chicken is hatched, and is taken up and enclosed in its belly, and by a channel made on purpose received by degrees into the guts, and serves instead of milk to nourish the chick for a considerable time" (p. 104). "That birds which feed their young in the nest, though in all likelihood they have no ability of counting the number of them, should yet (though they bring but one morsel of meat at a time, and have no fewer …. than seven or eight young in the nest together, which at the return of their dams, do all at once with equal greediness, hold up their heads and gape) do not omit or forget one of them ……. This seems to me most strange and admirable, and beyond the possibility of a mere machine to perform ……. *When they have laid such a number of eggs, as they can conveniently cover and hatch, they give over and begin to sit.*" However, that this behavior can be circumvented, as in domestic chickens, Ray learned from his friend Dr. Lister: "one and the same swallow, by the subtracting daily of her eggs, proceeded to lay nineteen successively and then gave over". On the subject of the growth of the young, Ray observed: "the marvellous speedy growth of birds that are hatched in nests ….. till they be fledged and come almost to their full bigness; at which perfection they arrive within the short term of about one fortnight, seems to me an argument of providence designing thereby their preservation, that they might not lie long in a condition exposed to the ravine of any vermin that may find them, being utterly unable to escape or shift for themselves" (p. 105). In building their nests, the adult birds "search out a secret and quiet place, where they may be secure and undisturbed in their incubation; then they make themselves nests, *every one after his kind*, that so their eggs and young may lie soft and warm, and their exclusion and growth be

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promoted. These nests, some of them so elegant and artificial, that it is hard for man to imitate them and make the like. I have seen nests of an Indian bird ….. which they hang on the end of the twigs of trees over the water, to secure their eggs and young from the ravage of apes and monkeys ….. After they have laid their eggs, how diligently and patiently do they sit upon them till they be hatched ….. with such an ardent and impetuous desire of sitting are they inspired, that if you take away all their eggs, they will sit upon an empty nest ….. After their young are hatched, for some time they do almost constantly brood them under their wings, lest the cold and sometimes perhaps the heat should harm them. All this while also they labour hard to get them food ….. with what courage they are at that time inspired, that they will even venture their own lives in defence of them. The most timorous, as hens and geese, become then so courageous, as to dare to fly in the face of a man that shall molest or disquiet their young ….. so eminent pieces of self-denial, must needs be the works of Providence, for the continuation of the species and upholding of the world: especially if we consider that all this pains is bestowed upon a thing which takes no notice of it, will render them no thanks for it, nor make them any requital or amends: and also, that after the young is come to some growth, and able to shift for itself ….. it takes no further care of it, but will fall upon it, and beat it indifferently with others."

"One necessary to the conservation of the species of animals; that is, the keeping up constantly in the world a due numerical proportion between the sexes of male and female, doth necessarily infer a superintending Providence. For did this depend only upon mechanism, it cannot well be conceived, but that in some ages or other there should happen to be all males, or all females; and so the species fail" (pp. 106–107).

Breeding times. Mr Boyle pointed out in his writings, "the conveniency of the season (or time of year) of the production of animals, when there is proper food and entertainment ready for them" (p. 108).

Instincts in animals. "I shall take notice of the various strange instincts of animals; which will necessarily demonstrate, that they are directed to ends unknown to them, by a wise superintendant. As, 1. That all creatures should know how to defend themselves, and offend their enemies; where their natural weapons are situate, and how to make use of them ….. A boar knows the use of his tushes; a dog of his teeth; a horse of his hoofs; a cock of his spurs ….. 2. That those animals that are weak, and have neither weapons nor courage to fight, are for the most part created swift of foot or wing, and so being naturally timorous, are both willing and able to save themselves by flight. 3. That poultry, partridge, and other birds, should at the first sight know birds of prey, and make sign of it by a peculiar note of their voice to their young, who presently thereupon hide themselves ….. 4. That young animals, as soon as they are brought forth, should know their food. As for example: such as are nourished with milk, presently find their way to the paps, and suck at them ….. 5. That such creatures as are whole-footed, or fin-toed, viz. some birds and quadrupeds, are naturally directed to go into the water and swim there, as we see ducklings, though hatched and led by a chicken, if she brings them to the brink of a river or pond of water, they presently leave her, and in they go, though they never saw any such thing done before; and though the hen clucks and calls, and doth what she can to keep them out: this Pliny takes notice of ….. every part in animals is fitted to its use, and the knowledge of this use put into them ….. 6. Birds of the same kind make their nests of the same materials, laid in the same order, and exactly of the same figure, so that by the sight of the nest one may certainly know what bird it belongs to. And this they do ….. though taken out of the nest and brought up by hand; neither were any of the same kind ever observed to make a different nest, either for matter or fashion ……. And therefore, as Dr. Cudworth saith well, they are not masters of that wisdom according to which they act, but only passive to the instincts and impresses thereof upon them" (pp. 110–113)

The migrations of birds. "I know not how to give an account of it, it is so strange and admirable. What moves them to shift their quarters? You will say, The disagreeableness of the temper of the air to the constitution of their bodies, or want of food. But how come they to be directed to the same place yearly, though sometimes but a little island …?…..The cold or the heat might possibly drive them in a right line from either, but that they should impel land birds to venture over a wide ocean, of which they can see no end, is strange and unaccountable: one would think that the sight of so much water, and present fear of drowning, should overcome the sense of hunger, or disagreeableness of the temper of the air. Besides, how come they to steer their course aright to their several quarters, which before the compass was invented was hard for man himself to do …….. Think we that the quails, for instance, could see quite across the Mediterranean sea? And yet, it is clear, that they fly out of Italy into Africa: lighting many times on ships in the midst of the sea, to rest themselves when tired and spent with flying ……. How these [salmon], when they have been wandering a long time in the wide ocean, should again find out and repair to the mouths of the same rivers, seems to me very strange, and hardly accountable, without recourse to instinct, and the direction of a superior cause" (pp. 113–114).

Nest hygiene. "In young birds that are fed in the nest, the excrement that is voided at one time is so viscid, that it

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hangs together in a great lump, as if it were enclosed in a film, so that it may easily be taken up, and carried away by the old bird in her bill. Besides, by a strange instinct, the young bird elevates her hinder parts so high ……. that she seldom fails to cast what comes from her clear over the side of the nest. So we see here a double provision made to keep the nest clean ……" (pp. 115–116).

"No birds of prey are gregarious. Again, that such creatures do not greatly multiply ……. They for the most part breeding and bringing forth but one or two, or at least a few young ones at once: whereas they that are feeble and timorous are generally multiparous, or if they bring forth but few at once, as pigeons, they compensate that by their often breeding, viz. every month but two throughout the year" (p. 121).

Adaptations of the body to the way of life. "I shall note the exact fitness of the parts of the bodies of animals to every one's nature and manner of living ….. woodpeckers .. have a tongue which they can shoot forth to a very great length, ending in a sharp stiff bony tip, dented on each side; and at pleasure thrust it deep into the holes, clefts, and crannies of trees, to stab and draw out coffi [larvae], or any other insects lurking there, as also into anthills, to strike and fetch out the ants and their eggs. Moreover, they have short, but very strong legs, and their toes stand, two forwards, two backwards, which disposition (as Aldrovandus well notes) nature, or rather the wisdom of the Creator, hath granted to woodpeckers, because it is very convenient for the climbing of trees, to which also conduces the stiffness of the feathers of their tails, and their bending downward, whereby they are fitted to serve as a prop for them to lean upon …… The swallow, whose proper food is small beetles, and other insects flying about in the air ….. is wonderfully fitted for the catching of these animalcules; for she hath long wings, and a forked tail, and small feet, whereby she is, as it were, made for swift flight ….. and she hath also an extraordinary wide mouth, so that it is very hard for any insect that comes in her way to escape her. ….. The colymbi, or douchers, or loons, whose bodies are admirably fitted and conformed for diving under water: being covered with a very thick plumage; and the superficies of their feathers so smooth and slippery, that the water cannot penetrate or moisten them: whereby their bodies are defended from the cold, the water being kept at a distance; and so poised, that by a light impulse they may easily ascend in it. That their feet are situate in the hindmost part of their body, whereby they are enabled, shooting their feet backwards, and striking the water upwards, to plunge themselves down into it with great facility, and likewise to move forwards therein. Then their legs are made flat and broad, and their feet cloven into toes with appendant membranes on each side; by which configuration they easily cut the water ….. Their bills are also made straight and sharp for the easier cutting of the water, and striking their prey. Could we see the motions of their legs and feet in the water, then we should better comprehend how they ascend, descend, and move to and fro; and discern how wisely and artificially their members are formed and adapted to those uses" (pp. 125–127).

"In birds all the members are most exactly fitted for the use of flying. First, the muscles which serve to move the wings are the greatest and strongest, because much force is required to the agitation of them; the underside of them is also made concave, and the upper convex, that they may be easily lifted up, and more strongly beat the air, which by this means doth more resist the descent of their body downward. Then the trunk of their body doth somewhat resemble the hull of a ship; the head, the prow, which is for the most part small, that it may the more easily cut the air, and make way for their bodies ….. That the train serves to steer and direct their flight, and turn their bodies like the rudder of a ship, is evident in the kite, who by a light turning of his train, moves his body which way he pleases ….. those that have long legs, have for the most part short tails; and therefore whilst they fly, do not, as others, draw them up to their bellies, but stretch them at length backwards, that they may serve to steer and guide them instead of tails. Neither doth the tail serve only to direct and govern the flight, but also partly to support the body, and keep it even" (pp. 127–128).

"…… the bodies of birds are small in comparison of quadrupeds, that they may more easily be supported in the air during their flight; which is a great argument of wisdom and design: else why should not we see species of pegasi, or flying horses, of griffins, of harpies, and a hundred more, which might make a shift to live well enough, notwithstanding they could make no use of their wings ….. Besides, their bodies ….. are also hollow and light; nay, their very bones are light: for though those of the legs and wings are solid and firm, yet have they ample cavities, by which means they become more rigid and stiff ….. Then the feathers also are very light, yet their shafts hard and stiff, as being either empty or filled with a light and spongy substance; and their webs are not made of continued membranes, for then had a rupture by any accident been made in them, it could not have been consolidated, but of two series of numerous plumulae, or contiguous filaments, furnished all along with hooks on each side, whereby catching hold on one another, they stick fast together …… And for their firmer cohesion, the wise and bountiful Author of nature hath provided and placed on the rump two glandules, having their excretory vessels, round which grow feathers in form of a pencil, to which the bird turning her head, catches hold upon them with her bill, and a little compressing the glandules, squeezes out and brings away therewith an oily pap or liniment, most fit and proper for the inunction of the feathers, and causing their little filaments more strongly to cohere …… And because the bird

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is to live many years, and the feathers in time would, and must necessarily be worn and shattered, nature hath made provision for the casting and renewing of them yearly. Moreover, those large bladders or membranes, extending to the bottoms of the bellies of birds, into which the breath is received [= the air-sac system], conduce much to the alleviating of the body, and facilitating the flight: for the air received into these bladders, is by the heat of the body extended into twice or thrice the dimensions of the external, and so must needs add a lightness to the body. And the bird, when she would descend, may either compress this air by the muscles of the abdomen, or expire as much of it as may enable her to descend swifter, or slower, as she pleases. I might add the use of the feathers in cherishing and keeping of the body warm ….. And for this reason we see, that water-fowls, which were to swim and sit long upon the cold water, have their feathers very thick set upon their breasts and bellies, and besides a plentiful down there growing, to fence against the cold of the water, and to keep off its immediate contact."

"That the tails of all birds in general do not conduce to their turning to the right and left, according to the common opinion, but rather for their ascent and descent, some modern philosophers have observed and proved by experiment ….. but in those that have forked tails, autopsy convinceth us, that it has this use ….. For it is manifest to sight, that the fork-tailed kite by turning her train sideways, elevating one horn, and depressing the other, turns her whole body. And doubtless the tail hath the same use in swallows, who make the most sudden turns in the air of any birds, and have all of them forked tails" (pp. 129–131).

"I shall now add another instance of the wisdom of nature, or rather the God of nature, in adapting the parts of the same animal one to another, and that is the proportioning the length of the neck to that of the legs ….. the necks of birds and quadrupeds are commensurate to their legs, so that they which have long legs have long necks, and they that have short legs short ones …. Only in these too there is an exception, exceeding worthy to be noted, for some water-fowl, which are palmipeds, or whole-footed, have very long necks, and yet but short legs, as swans and geese ….. wherein we may observe the admirable providence of Nature. For such birds as were to search and gather their food, whether herbs or insects, in the bottom of pools and deep waters, have long necks for that purpose, though their legs, as is most convenient for swimming, be but short ….. Whereas there are no land-fowl to be seen with short legs, and long necks, but all have their necks commensurate to their legs ….. For Nature makes not a long neck to no purpose" (pp. 136–138).

"Lastly, another argument of providence and counsel relating to animals, is the various kinds of voices the same animal uses on divers occasions, and to different purposes. Hen-birds, for example, have a particular sort of voice, when they would call the male; which is so eminent in quails, that it is taken notice of by men, who by counterfeiting this voice with a quail-pipe, easily draw the cocks into their snares. The common chicken all the while she is broody sits, and leads her chicks, uses a voice which we call clucking. Another when upon sight of a bird of prey, or apprehension of any danger, she would scare them, bidding them, as it were, to shift for themselves, whereupon they speedily run away, and seek shelter among bushes, or in the thick grass ….. These actions do indeed necessarily infer knowledge and intention of, and direction to, the ends and uses to which they serve; not in the birds themselves, but in a superior agent, who hath put an instinct in them of using such a voice upon such an occasion; and in the young of doing that upon hearing of it ……. Other voices she hath when angry, when she hath laid an egg, when in pain, or great fear, all significant ….. which yet are all argumentative of Providence, intending their several significances and uses" (pp. 138–139).

Leonhard Baldner (1612–1694) was a Strasbourg fisherman and councillor who commissioned paintings from Johann Jakob Walther, a well-known artist of that city, for his *Vogel-, Fisch- und Thierbuch* (1646–1687) [*Bird, fish, and animal book*], in which he made a zoological inventory of the Rhine and its surroundings that included 72 birds, 45 fish and crustaceans, and 52 other animals. When Willughby and Ray passed this way in 1663 they purchased copies of the text and some paintings by Baldner that can still be seen in London. See Baldner (1973).

Birkhead & van Balen (2008) demonstrated the important, but largely unrecognized role of European bird-keeping in the development of several different areas of bird study, especially song acquisition, function and anatomy, territorial behaviory, breeding biology, external genitalia, migration, instinct, and learning.

(3.) The foundations of field ornithology: early and mid-18th century

Physico-theological or natural theological ideas spread at the beginning of the 18th century from England (see above) and Holland to Germany, mainly to the Protestant areas. Their supporters endeavored to attain knowledge of God, independent of scripture but through the study of nature, regarded as untainted by human activity (Krolzik 1980, 1996; Waschkies 1988; Jahn 1989, 1998: 7–8, 2000; Bäumer 1996: 197). On the basis of their investigations of useful, orderly, or simply beautiful structures (adaptations) or processes in nature, the existence and properties of God, His power, wisdom, and goodness, could be demonstrated or inferred. These concepts induced large numbers of European naturalists in the 18th century to leave their libraries and go into the field to carry out studies on living molluscs, insects, frogs, birds, and other an-

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imal groups, as well as plants. They were, following John Ray, physico-theologians; in Germany for instance, the well-known naturalists J.A. Fabricius, F.C. Lesser, A.J. Roesel von Rosenhof, H.S. Reimarus, C.K. Sprengel, J.R. Forster; ornithologists like A. von Pernau, J.L. Frisch, and J.H. Zorn. The physico-theological philosophical framework of these researches led to important discoveries concerning adaptations of plants and animals clearly "designed" for a purpose, the ways of life of an assortment of animals, and also the close adaptive relationships between flowering plants and insects with respect to pollination (C.K. Sprengel). The clear "adaptedness" and harmony of many natural phenomena were taken as proofs of the existence of a wise Creator ("Argument from Design"). Nature study was divine worship, and nature was "read" as the book of God's creation. Later, the wealth of biologically significant results gathered by these enthusiasts could simply be transferred to modern biology, following the replacement of the physico-theology of the field naturalists of the 18th and 19th centuries with the new evolutionary paradigm (Mayr 1984: 86).

William Derham, a student and friend of John Ray in England, published in 1713 an important book on *Physico-Theology* (see References for full title), which appeared in a German translation in 1730: *Physiko-Theologie oder Natur-Zeitung zu GOTT [Physico-Theology or Nature Reports to GOD]*. It contains observations on the Earth, on animals in general, on mankind, quadrupeds, birds, insects, crawling animals, and on plants. In the chapter *Observations of Birds*, the clear fitness for purpose of the form and structure of the body, and of the wings for flying, is discussed. The legs of wading bird are naked and long; the feet of swimming species have webs; those of raptors have curved talons and also the bill is hooked, both for seizing and holding prey; a supporting tail and short legs serve woodpeckers well in climbing trees. The interlocking barbules of feather vanes, with their hooklets, which Derham observed through a microscope, are precisely described and illustrated. He wrote that migratory birds know when to start their journey and when to return, and that the Creator has determined these times and given the birds an instinct when to begin migration and which route to fly, across alien seas and countries. The artistic and purposeful structure of their nests, and the great variety that exists, the different nest sites in trees, on the ground, on rocks, etc., and the natural instinct to choose the appropriate site at the right time of year are all described in great detail. All these works "shine forth with the great Creator's infinite wisdom, counsel, and providence" (p. 902, 1741 edition).

The tendency of ornithologists in the 18th and 19th centuries to concentrate *either* on the systematics of birds *or* on their natural history (way of life) led to a fundamental bifurcation in the science, which was to persist for a period of over 200 years (Haffer 2006, 2007a; see Fig. 2 above). However, Blasius Merrem did attempt, in his fragmentary outline of ornithology in 1788, to unite both research traditions. There were field ornithologists who also occupied themselves with problems of systematics, (e.g.) J.L. Frisch in the text to his large folio work of 1733–1763, J.M. Bechstein, who introduced many scientific names into the literature, and in the 19th century C.L. Brehm, the discoverer of several European sibling species (Firecrest/Goldcrest, Marsh/Willow Tit, Eurasian/Short-toed Treecreeper, Crested/Thekla Lark), who thought much about intraspecific variation. But such connections were insufficient to effect an integration of the two branches of ornithology, which remained widely separated until into the 20th century (Haffer 2007a, 2008).

In the following section we will look at the species knowledge of the field ornithologists J.F.A. von Pernau, H.F. von Göchhausen, J.L. Frisch, and J.H. Zorn, as well as of the systematist J.T. Klein. It must be borne in mind that the field ornithologists mentioned here dealt with the local fauna of their respective native regions, and described the habits of only those species that they had personally observed, while Klein's ambition was to compile from the literature a list of the bird species of the world, without himself having had much field experience. He had no personal knowledge of most of the species on his list.

The first ethologist – Ferdinand Adam von Pernau (1702, 1720). Von Pernau lived from 1660 to 1731. He did not wish to create a complete avifauna of southern Germany with his books, but instead only to report on his personal observations of those species that he saw and studied in the surroundings of his home area of Coburg (Franken). What are mainly absent are the songbirds and some game-birds, and he mentioned only a few water and wetland species in his writings. Pernau too saw manifestations of God's work in nature's creatures. He developed individualistic and astonishingly modern ornithological hypotheses and arrived at his own independent judgements.

J.F.A. von Pernau was a senior civil servant at the royal court of Sachsen-Coburg, but when his government work allowed him some free time he used it for intensive biological studies of birds. His intention was to stimulate admiration for God's creatures and to help the reader onto "the path to redemption out of frivolous pleasure-seeking and dishonorable gluttony" (Stresemann 1951: 289). There is no known portrait of this important figure. Pernau's book of 1702 had the lengthy title *Unterricht, Was mit dem lieblichen Geschöpff, denen Vögeln, auch ausser dem Fang, nur durch Ergründung deren Eigenschafften und Zahmmachung oder anderer Abrichtung man sich vor Lust und Zeitvertreib machen könne* [*Lesson on what can be done, for pleasure and amusement, with those delightful creatures, birds, in addition to catching them, only by inquiring into their qualities and taming or otherwise*

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training them] (Fig. 13). A follow-up volume appeared in 1720 under the title *Angenehme Landlust, deren man in Staedten und auf dem Lande, ohne sonderliche Kosten, unschuldig geniessen kann* [*Agreeable country pleasures that may be innocently enjoyed in town and country, without exceptional expense*]. These books greatly influenced ornithology in the 18th century, and most hunters, fowlers and bird-keepers were familiar with them, which was less the case among naturalists. They were published anonymously, reaching ten editions between 1702 and 1797. However, the name of the author was known to several of his writing contemporaries, including Wetzel, von Göchhausen (see his entry on Chaffinch below), Wirsing, and von Dießkau (see Schlenker 1982a). Later, Stresemann (1925) was the first to rediscover Pernau's writings and stress their importance in the history of ornithology (see also Stresemann 1947, 1951, 1962). Pernau differentiated bird species based on the manner in which they feed, their preferred habitat, the degree of their sedentariness (non-migratory, partially migratory, migratory), their choice of nest site, their sociability during and following the breeding season, their manner of bathing, or the way in which they feed their young (from the crop or from the bill), and it was Pernau who made the first explicit comments on song learning in finches. He was both a bird-keeper and field naturalist, discussing a few songbird species, notably the Chaffinch. He speculated about the function of territory as an exclusive source of food, suggesting that the Nightingale "is forced for the sake of her feeding requirements to chase her own equals away, for if many were to stay together they could not possibly find enough worms and would inevitably starve" (Fig. 14).

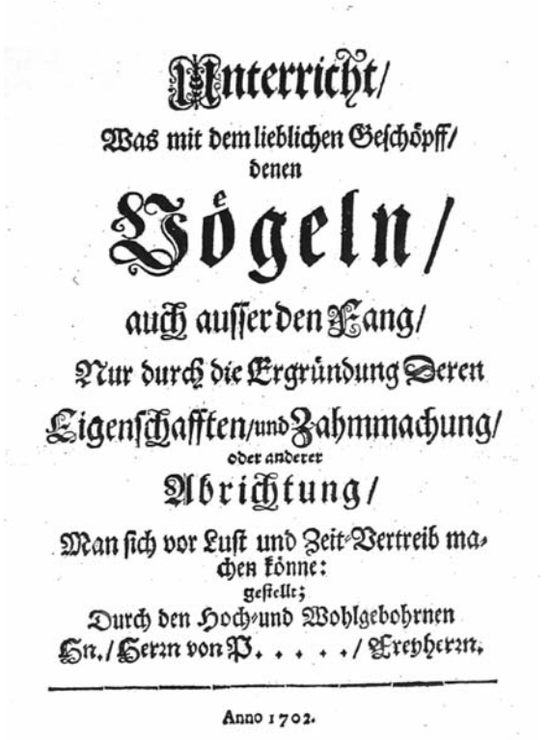
Unterricht/
Was mit dem lieblichen Geschöpff/
denen
Vögeln/
auch ausser den Fang/
Nur durch die Ergründung Deren
Eigenschafften/und Zahmmachung/
oder anderer
Abrichtung/
Man sich vor Lust und Zeit-Vertreib machen könne:
gestellt;
Durch den Hoch- und Wohlgebohrnen
Hn./Herrn von P. . . . . /Freyherrn.
Anno 1702.

Fig. 13. Title page of von Pernau (1702; from 1982 reprint).

Pernau recognized territorial behavior in birds and its biological significance, and postulated that a migratory bird is not driven to depart by hunger or cold but "is driven at the right time by a secret impulse which it obeys, in contrast to humans, who often resist such impulses" (Stresemann 1947, 1951). Pernau used behavioral traits as an aid to taxonomy (e.g., tail wagging in both wagtails and pipits) and noted that unmated male songbirds sing more than mated ones. He also interpreted the biological importance of bird calls, (e.g.) that the rain-call of the Chaffinch has a warning, territorial-defense function. His statements on how a bird learns its own song were confirmed by later workers. His ideas on the function of song, how much is learned and how much is innate, the inheritance of "traditional" song dialects and their patterns, and on imprinting were all of fundamental significance (Thielcke 1988). Pernau's books indicated the future direction and aims of avian biological research; he and Emperor Friedrich II of Hohenstaufen were really the founders of scientifically conducted biological field studies of birds. In the originality of his work he can be compared with the founders of ethology Altum and Heinroth in Germany, and Selous and Howard in England (Stresemann 1925: 612, 621; 1947, 1951).

J.M. Bechstein had also recognized the value of Pernau's contribution, editing the ninth and tenth editions of his book. Bechstein wrote in his foreword that "there has not been a bird book until now, excepting Zorn's '*Petinotheologie*', in which the practical natural history of these animals has been presented more completely and with many interesting observations than this one". He was very surprised, therefore, to find it so little referred to in writings on ornithological systematics (see the anonymous review of this edition in *Allgemeine Literaturzeitung* Vol. 1, no. 66, pp. 524–525, February 1799).

***Oberjägermeister* Hermann Friedrich von Göchhausen (1710, 1732).** Von Göchhausen was baptized on 5 March 1663 and died in Weimar as *sächsisch-weimarischer Oberjägermeister* in 1733 (Schlenker 1994). This naturalist was especially interested in the avian world and published his findings on 104 species in a book with the impressive title:

Notabilia venatoris,
oder Jagd- und Weidwercks-Anmerckungen [...] aufgezeichnet von einem die Jägerei liebenden Waidemann in Weimar, welcher gerne in Wäldern hörete frühe der Vögel Gesänge [...] [*Hunting and sporting remarks set down by a lover of the noble sport in Weimar, whose pleasure*

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Fig. 14. Frontispiece of von Pernau (1702; from 1982 reprint).

it is to listen to the song of the woodland birds at dawn].

This work appeared for the first time in 1710 (Fig. 15) and subsequently in ten further editions; we have made use of that of 1732. For most species, especially the game-birds, the huntsman gives details on breeding, food, and migration, as well as incubation period and clutch size, these last not always being correct, most likely because he occasionally relied on hearsay. Nevertheless, Göchhausen made a considerable contribution to the dissemination of ornithological knowledge in Germany (Stresemann 1925, 1926b). Of particular interest is his information on the breeding of the Little Bustard in Sachsen-Weimar (see under *Brach-Vögel*).

In his book, Göchhausen deals firstly with the mammals, followed by "On breeding birds" (pp. 70–163), divided into landbirds, waterbirds, and birds of prey. The next chapter is on trees (pp. 164–251) and the last, "On hunting", contains details of the equipment and authority of the hunter plus remarks concerning the "properly designed deer park" (pp. 279–2282). Several appendices deal with instructions for hunting and forestry workers, lark-trapping with nets, and with the known fish species in the regions belonging to Saxony.

On Breeding Birds

A selection of the interesting comments by the author follows below, mostly in summarized form but some as unabridged quotations. For each species Göchhausen gives a short description of plumage, but that is omitted here. Species order is as given by the author and therefore differs from that in online Appendix 2.

Auer-Hahn [Capercaillie]: Eats the buds of beech trees in winter; treads the female after display. She raises the young without the help of the male. Also eats berries in summer (pp. 70–74)

Trappen [Great Bustard]: "In the summer this bird eats the green unripe grain of cereals, later in the year only the ripe grain, and in winter the seeds of cereals and root-crops. What is notable is that if it has the opportunity, it will also take larks and other small birds, or newly-hatched chicks of domestic hens or quails, causing much harm.

The Great Bustard lays its eggs often in fields of oats in spring, selecting those areas furthest from tracks and paths, where it digs a depression in the bare earth to lay its eggs in, never more than two. These are yellowish white with a size between those of Turkey and goose eggs. What is remarkable is that although the Great Bustard is a timid bird it will sit fast on the eggs until forced from the nest,


NOTABILIA
VENATORIS,
Oder
Jagd- und Weidwercks-
Anmerckungen/
Wie es zeithero bey der Löblichen Jägerey insgemein gehalten / welche Dinge practicabel oder impracticabel geachtet / und was vor Gebräuche und Gewohnheiten theils Orthen eingeführet und gewiesen worden /
Auch
Wie vielerley Orthen derer Gehölze hin und wieder in Waldungen sich finden / wie dieselben nutzbarlich abzuholtzen und zu gebrauchen / auch andere unterschiedliche / einem Forst-Bedienten zu wissen / nöthige Sachen /
Nicht weniger
Aller bekandten Vogel Eigenschafften / so viel man aus der Erfahrung wahrgenommen hat /
Aufgezeichnet von einem
Der Jägerey-liebenden Weidemann /
Welcher gerne in Wäldern
Hörete Frühe der Vögel Gesänge.
Nordhausen / zu finden bey Carl Christian Neuenhahn. 1710.

Fig. 15. Title page of von Göchhausen (1710).

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whereupon it does not leave the eggs in the same place but carries them away (probably under its wings or with its sinuous neck) to a distance of around 100 paces where they are incubated again, as long as the bird is not further disturbed, for a total of four weeks [= incubation period 21–26 (–28) days], then leads the young as soon as they can walk to safety in the cereal crop. Otherwise it is conspicuous as a bird of autumn, since it remains here when other wild birds leave, to return in the spring. The Great Bustard moves around seeking the warmer fields, feeding in winter time on the vegetation mentioned above."

The courtship display of the Great Bustard "takes place in Lent, and if the male has not just one hen but several, like the Capercaillie, he spreads his feathers and tail like a Turkey, but unlike the Capercaillie he makes no sound during this display. At this time it is one of the most bad-tempered of birds, often kicking and striking each other." "….. when the male is old he has a finger-long beard of two or three long, thin white feathers, which, when he is angry, is spread out on each side of his head to give himself an impressive appearance" (pp. 74–77).

Birck-Wildpret [Black Grouse]: Displays on trees as well as on the ground; raises his feathers like a Turkey and jumps up from the ground. The hen is mostly nearby. Nest is on the ground, 8–12 eggs. Food in winter is birch buds and shoots, in summer berries and plants. Males and females are very differently colored (pp. 77–80).

Hasel-Hun [Hazel Grouse]: In old conifer forest where hazel trees grow; eats catkins, buds, later berries and plants. Male and female are similarly colored, but the former is larger with a black throat. Courtship takes place at Lent; the display call is a whistle. Nests on the ground, and incubates the eggs for three weeks [correct is 22–25 days], 6–8 young, stays in the breeding area during winter and does not migrate (pp. 80–82).

Rebhun [Grey Partridge]: Incubates eggs for three weeks [correct is 24–25 days], has 16–18 young that are raised without any help from the male; food is seeds and fruits, in winter green seeds mixed with gravel and sand (pp. 82–83).

Wachtel [Common Quail]: The 7–10 young are reared by the female only (p. 83).

Waldschnepfe [Woodcock]: "this bird can open and close just the end […] , about a thumb's breadth, of its bill (which is as long as a finger) just like a pair of pliers, which is made possible by certain nerves in the bill supplied by nature which no other bird possesses, and this can be demonstrated on a dead Woodcock if the head is squeezed"; 3–4 young; migrates at night (pp. 84–85).

Brach-Vögel [fallow-land birds]: The most important faunistic record made by Göchhausen is of the breeding of Little Bustard (*Tetrax tetrax*) in Sachsen-Weimar (Kunz 1902; Stresemann 1926a: 691). He writes: "There are three fallow-land birds. Firstly, the one called *Keilhacken* or *Fasten-Schlier* [= *Little Bustard*], a bird around the same size as a sickly (?) [*verkühlet*] Turkey, and colored like a Great Bustard, with long feet so that they run as fast as an arrow, and sometimes they press themselves close to the ground and are quite hidden. The proportion and form of the bill and head are very like a Great Bustard and they also fly as fast as an arrow, and make a high whistle call. They migrate through our country in autumn and spring, but do breed very rarely here, where they have been found on fallow fields and between stones. They have two young, and can only be obtained using a shotgun. They feed on the smallest animals, especially earthworms."

Secondly, the *Saat-Hun [= European Golden Plover]*, as big as a pigeon, with speckled greenish feathers, in flocks on newly sown cereal fields in the autumn; passage migrant.

Thirdly, the *Ditgen [= Dotterel]*, smaller and with a whiter belly than the Golden Plover, and also an autumn passage migrant on newly sown fields. (pp 85–86).

Kibitz [Northern Lapwing]: Appears first in the spring; has a bill like a pigeon; attacks people in the breeding season; has a feather crest like a heron and eggs that are good for eating; 3–4 young. Incubation period 14 days [correct is 27 days]; feeds on larvae, worms, etc. (p. 87).

Ringeltaube [Wood Pigeon]: Timid; nest made of few materials on oak or spruce tree and never has more than two young (pp. 87–88).

Hohltaube [Stock Dove]: Has no white neck-ring, rather bluish in color, nests in holes in trees (p. 88).

Turteltaube [Turtle Dove]: The smallest dove, with a white band at the end of its tail; breeds in trees, male and female together (p. 89).

Tages-Schlaffe [Nightjar]: Short bill, at the head very broad; shaped like a swift; active at twilight and lays 4 speckled eggs [error; never lays more than 2]; leaves us to migrate in autumn (p.90).
This species was not included in the first edition of 1710.

Krammets- or *Krannebet-Vogel [Fieldfare]*: Feeds on juniper berries; winter visitor, breeds in the east. Often appears with the Redwing and is caught in large numbers in snares (p. 91).

Schnerr [Mistle Thrush]: Breeds in oaks and other trees (like Blackbird and Song Thrush) and has 3–4 young,

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feeds on mistle and juniper berries. Male and female very similar in coloration (p. 92).

Meer-Amßel [Ring Ouzel]: "This species of bird does not nest in our region and passes through in autumn and spring like other birds. It is a black-gray bird, a little speckled, and slightly larger than the Blackbird, with a white throat, almost like a Dipper. It migrates on powerful wings, but is a very stupid bird on the trapping ground, according to fowlers; when it is caught by stalking […] it allows itself to be caught again" (pp. 92–93).

Stein-Amßel [Rock Thrush]: Lives like Northern Wheater in rock clefts, cliffs, and vineyards but is as big as a Golden Oriole, "ash-colored from the head to the rump, the belly brick-red, speckled slightly with white, tail red, and chestnut brown on back and wings with the feathers slightly dusted white", feet brown as are bill and eye. Feeds on worms, etc. and grapes; breeding similar to Wheatear and departs in autumn. This species "is little noted in our region" hence is very rare (pp. 93–94).

Zipp-Drossel [Song Thrush]: Common breeding bird on trees, incubation period 14 days, 4–5 young; migratory bird (pp. 94–95).

Schwartz-Amßel [Blackbird]: The male is blacker than the female and with a wax-yellow bill and yellow eye-ring; incubation period 14 days, 4–5 young. Some of the Blackbirds remain in winter (p. 95).

Wein-Droßel [Redwing]: Has red under the wings; feeds on berries, snails, larvae, and worms; passage bird (p. 96).

Staar [Common Starling]: Breeds in holes; migratory bird (pp. 96–97).

Weyhrauch- or *Kirsch-Vogel [Golden Oriole]*: Egg-yolk-yellow with black wings; returns in late spring. Feeds on cherries and worms, etc. "Forms its nest with wool and bast [= fibers from the phloem of plants] gathered together, on the fork of a branch, bound to the legs of the fork with long strips of bast from lime trees and so cunningly constructed that it hangs like a long pouch or like a church collection bag, so that it is a marvel to see." Incubation period 14 days [correct is 15–16 days], 3–4 young (pp. 97–98).

Grienitz or *Grienitz-Vogel [Common Crossbill]*: Breeds in the winter (January–February) in conifer forests, where the nest is in high spruce trees, 4–5 young. In their first year they are gray and slightly greenish, in the second year reddish, in the third yellow-green. Some have the upper mandible crossed to the left, others crossed to the right. People talk of larger and smaller Crossbills but that is not true. They arrive when the conifer cone crop has been good. "Regarding the breeding of Crossbills, the reason why the young are hatched at the coldest time of year could be that they do not arrive here only in the spring but also in the autumn, and indeed come then in greater numbers, most arriving when the fir cone crop is a good one in our region because fir seeds are its favorite food. And when these oil-rich seeds are sufficient to last into the winter then the bird eats so many it puts him into the mood for mating" (pp. 98–99).

Seiden-Schwantz [Bohemian Waxwing]: Appears regularly but is not a breeding bird; its food is juniper berries (pp. 99–100).

Kern Beisser [Hawfinch]: Bill thick, breeding bird, 4 young, many Hawfinches spend the winter here (pp. 100–101).

Gümpel, Blut-Finck, Thum-Pfaffe or *Rothschlegel [Bullfinch]*: Eats rowan berries, 4 young, "which can easily learn to whistle whatever you want them to" (pp. 101–102).

Lerche [Sky Lark]: Common; usually breeds twice in summer (pp. 102–103).

Heide-Lerche [Wood Lark]: Tail shorter than in the last species, breeds in clearings in the forest, 4–5 young (pp. 103–104).

Mantel-Krähe or *Blarack [European Roller]*: Blue, back brownish, rare passage bird, does not breed here (p. 104).

Schwartz-Specht or *Hohl-Krähe [Black Woodpecker]*: Breeds in holes it makes itself, 3–4 young, remains in winter. Tail has stiff supporting feathers; 2 toes pointing forwards and 2 backwards (pp. 105–106).

Grün-Specht [Green Woodpecker]: Stays here in winter also (p. 106).

Bund- or *Roth-Specht [Great, Middle(?), and Lesser Spotted Woodpeckers]*: "There are three different kinds of three different sizes", black-and-white checkered, red on the head and under the tail.

Perhaps alongside Great Spotted and Lesser Spotted, Göchhausen here also distinguished Middle Spotted Woodpecker (p. 107).

Blauspecht [Eurasian Nuthatch]: Breeds in holes in trees and remains here in winter (p. 107).

Baum-Reiter [treecreeper]: With thin bill, curved at the tip, breeds in hollow trees (p. 108).

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Wiedehopff [Hoopoe]: Forages for its food like a snipe, departs already in August and is the last to return (pp. 108–109).

Nachtigall [Common Nightingale]: Breeds in thorny hedges (pp. 109–110).

Wendehalß [Wryneck]: Migratory bird, its call is similar to the Common Kestrel; breeds in hollow trees. It has a long tongue with little barbed hooks like a woodpecker (pp. 110–111). This species was not included in the first edition of 1710.

Roth-Kehle [*Robin*]: A well-known common bird (pp. 111–112).

Roth-Schwantz [Common Redstart]: Breeds in old trees (pp. 112–113).

Fliegen-Schnepper [one of the Sylvia *species]*: A little gray bird, creeps around in hedges and bushes; breeds in bushes or hedges (p. 113).

Graß-Mücke [Whinchat]: "This little bird is as big as a Robin, but has a short tail and is speckled gray in color with a yellowish belly, almost always found on meadows where it searches for food in the grass and in bushes, under which it lays its eggs and raises its young. Has usually 4 to 5 young, but what is remarkable is that, where other birds have differently speckled eggs, this bird has pure sky-blue eggs. Eats only flies, larvae, and worms and because it is the first to leave on migration it returns very late to the same place since it cannot stand the cold" (pp. 112–113).

Stein-Klatsche [Northern Wheatear]: Related to the Whinchat and with a similar shape, whiter on the belly, but the Wheatear prefers bare barren land and stony places to meadows; breeds in holes and lays 4 white slightly speckled eggs, feeds on worms and larvae and is migratory (pp. 114–115).

Finck [Chaffinch]: "Herr Bernauer [= A. von Pernau] especially explains in his description how this bird can be trained to utter a great variety of different songs, and he himself has observed how this variety is produced" (pp. 115–117).

Buch-Finck, Quecker or *Zährling [Brambling]*: Colors more attractive than in Chaffinch; winter visitor (p. 117).

Stieglitz and *Hänffling [Goldfinch* and *Linnet]* (pp. 117–119).

Schwanschel or *Grünling [Greenfinch]*: Food is seeds (hemp seeds) (p. 119).

Zeißig [Siskin]: The nest is in high conifer trees; found here in summer and winter (pp. 119–120).

Zitscherling [Common Redpoll]: Winter visitor (p. 120).

Meißen [tits]: Great Tit [Pickmeiße] is the biggest; others are Crested Tit [Kupp-Meiße]; Blue Tit; Coal Tit [Schwartz-Meiße]; Long-tailed Tit (pp. 121–122).

Bachstelzen [wagtails]: (1) Gray and white, throat black [= White Wagtail] and (2) underparts yellow, pale gray, back mixed with yellow [= Yellow Wagtail] (pp. 122–123).

Aemmerling [Yellowhammer]: Common (pp. 123–124).

Holtz-Muschel or *Wilder Sperling [Tree Sparrow]*: Breeds in hollow willows and remains in winter (pp. 124–125).

Zaunkönig [Wren]: Sings loudly and builds a large nest of moss with a small entrance (pp. 125–126).

Weiden-Zeisig [Chiffchaff] and *Gold-Hähnichen [Goldcrest/Firecrest]* (p. 126).

Waterbirds

Schwaane [Mute Swan]: Incubation period 4 weeks [correct is 35–38 days] (pp. 130–131).

Wilde Ganß [Greylag Goose]: Incubation period 4 weeks [this is correct; 27–29 days] (p. 131).

Fisch-Reiher: The well-known gray-colored herons that nest on high trees; in addition (1) large heron, light gray on the back, white on the body speckled with black streaks, bill long and red, feet yellow, with 2–3 long feathers on the head *[= Grey Heron]*, and (2) smaller heron, dark gray on the back, black on the head, bill black, feet short and blue; 2–3 long feathers on the head *[= Night Heron]* (pp. 132–133).

Storch [White Stork]: Widespread in the villages (pp. 133–134).

Schwartzstorch [Black Stork]: Bill and legs reddish; lives in forests; incubation period 3 weeks [correct is 30 days] (p. 134).

See-Rachen [Goosander]: White, head black (p. 134).

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Gemeine grosse wilde Ente [Mallard]: Breeds on willow trees, even in Crow or Magpie nests near lakes or rivers, "to which they later take their fledged young (which takes 3 weeks) from these willows or other trees, probably carrying them carefully in their bill, so that they are in safety". Migratory, but many stay here in the winter (p. 135).

Schmal-Endte: Similar to the large duck (above) but smaller (p. 136).

Pfeiff- or *Speck-Endte [Eurasian Wigeon]*: Head brown, belly white, wings brown with white patches (pp. 136–137).

Horbel or *Bläßlein [Coot]* (pp. 137–138).

Taucher or *Wasser-Huhn [Great Crested Grebe]* (p. 139).

Ried-Schnepffe [Great Snipe]: "This bird is as big as a Woodcock and is as great a delicacy, and has also the same color and form, but in flight it is much faster. It migrates like other birds after it has raised its 4 to 5 young here in the largest swamps and marshes, and nowhere else. Its food is also the same as the Woodcock, namely the white tender roots of plants they find in the marshes" (pp. 139–140).

Haarschnepffe [Jack Snipe]: "This is rather smaller than the previous bird, but however in color and nature is just the same" (p. 140).

Pfuhlschnepffe or *Himmelsziege [Common Snipe]*: "There is no difference in color to the previous but one bird, only that species is larger and this one is different in that, when it is disturbed, it climbs up high into the air then, when it flies in an arc back towards the ground, it makes such a loud quivering sound, which they say is made by the wings, that one is amazed by it. When it sits on the ground, by water and in marshes, it often makes a call when the weather changes that has two different notes. It breeds in swamps and on hillsides, without nesting material, laying four eggs which are incubated in 14 days" [correct is ca. 19 days] (pp. 140–141).

Sandläuffer or *Grießhun [Little Ringed Plover]*: Speckled black with white breast; breeds on sandbanks; ringing call (p. 141).

See-Schwalbe [terns]: "There are two of these though they are the same color, silvery white, but one of them is larger than the other. The larger one swims now and then on the water like a duck, which the smaller one never does but instead flies up and down the whole day long like a swallow, over the lakes and ponds, looking for its food, which is small water animals. They breed in our region in reedbeds and have 3 to 4 young, but migrate like other birds" (p. 142).

Eiß-Vogel and *Wasser-Amßel [Common Kingfisher* and *Dipper]*: The food of both is worms and snails and both stay here during winter where there is open water (pp. 142–143).

Rohr-Dommel [Eurasian Bittern]: Calls at twilight and at night, and can be heard a long way away (pp. 144–145).

Rohr-Sperling [Reed Bunting]: Breeds in reedbeds, moves away in autumn (p. 145).

Birds of Prey

Males are generally smaller than females, many regurgitate pellets. They never drink and survive on the liquid in their food.

Steinadler [Golden Eagle]: Takes roe deer and hares; nests in the forest and has 2 young (pp. 146–147).

Schuhu [Eagle Owl]: Nests on cliffs, takes hares. Remains here in winter (pp. 147–148).

Blau-Fuß [Peregrine Falcon]: "Although the Peregrine Falcon is not much larger than the Goshawk, it has a great advantage in its talons and bill since with these it easily catches hares, ducks, and partridges. Unlike other birds of prey, it does not seize them at the first strike but knocks them to the ground with its feet, and only then does it grasp them with its talons. It nests in our region in forests as well as on old ruined towers and walls. Because of its skillful way of killing it is much sought after by falconers, who use it to hunt hares and ducks, and they catch them in nets and by using a leather 'saddle' attached to pigeons. It moves away in the autumn" (pp. 148–149).

Habicht [Goshawk, male]: They leave in autumn and return early in spring. In the forest they look for their old nests, where they are least disturbed, 2–4 young, "which hatch after 14 days" [correct is 35–38 days]. They are used by men to catch partridges, quail, hares, and herons (pp. 149–150).

Sperber [Sparrowhawk, female]: Slightly smaller than the Goshawk; is used by men to hunt partridges, quail, and songbirds (p. 150).

Baum-Falcke [Hobby]: "Although there is no difference in size, nest, or migration between the Sparrowhawk and this falcon, there is a difference in color for this bird is bluish on the back, yellowish on the throat and black in

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between. The young leave the nest very late, around St. James's Day [25 July]; they can be very useful in catching larks. […] This falcon has the habit that, when it sees a hunter or anyone with dogs in a field, it stays close to them and flies above them, so that if a lark or so is disturbed and flies up then it can pursue it" (pp. 150–1151).

Schmerl [Sparrowhawk, male]: Nests rarely here. "This is a small, delicate, barred-breasted bird, yellow feet, as large as a Fieldfare" (pp. 151–152).

Rittel-Geyr [Common Kestrel]: Its food is mice, voles and young birds, nests on church towers; migratory bird (p. 152).

Horneule [Long-eared Owl] and *Steineule [Barn Owl]*: The former prefers to nest in hollow trees, the latter in old buildings; both live on mice and voles and regurgitate pellets; they do not move away in winter (pp. 152–153).

Mülane or *Schwalben-Schwantz [Red Kite]* (p. 153).

Mäuse-Geyer [Common Buzzard]: Feeds on mice, voles, frogs, young hares, and also on carrion (pp. 153–154).

Fisch-Geyer [Osprey]: Their food consists only of fish; they migrate in autumn (p. 154).

Kautz [Tawny Owl] and *kleiner Stein-Kautz [Little Owl]* (pp. 155–156).

Neun-Tödter [shrikes]: There are two species, (1) Wild- or Krück-Elster, rather larger and catches young birds *[Great Grey Shrike]*; (2) a smaller species which feeds on beetles and butterflies that it impales on the thorns of hawthorn and blackthorn trees; nests in thorny bushes *[Red-backed Shrike/Lesser Grey Shrike?]* (p. 156).

Kuckuck [Common Cuckoo]: Feeds on caterpillars and worms, does not have curved talons and has small feet like a pigeon; in the autumn does not change itself into a Sparrowhawk. "…. Although they mate and produce young they never lay their eggs in a nest they have made themselves, but lay them in the nests of other birds, like Whinchat, wagtail and such birds, and then let them feed their young with worms, etc. and raise them" (pp. 157–158).

Nuß-Heher [Eurasian Jay]: A common woodland bird (pp. 158–159).

Tannen-Heher [Nutcracker]: Lives in fir forests, eats fir and spruce seeds [no remarks are made on breeding occurrence] (pp. 159–160).

Golck-Rabe [Common Raven]: A harmful bird which does not leave in winter (p. 160).

Kleiner Rabe [Carrion Crow]: Smaller than the Raven, nests in woodland and gardens and is shot while on the nest. "But the crow that is gray on the body [= Hooded Crow] does not nest in our region but comes here on migration and stays, since it has the same habits as the other crow, until spring" (p. 161).

Rücken [Rook]: Colony breeder; feeds on seeds and larvae, worms, etc. (pp. 161–162).

Dohle [Western Jackdaw]: Nests in holes in walls; does not leave in the winter (p. 162).

Aglester [Magpie]: Cunning and harmful. The nest is domed and has an entrance at the side (pp. 162–163).

The first book of folio plates of Central European birds – Johann Leonhard Frisch (1733–1763). The subrector and later rector of the famous grammar (or high) school "Zum Grauen Kloster" in Berlin was a versatile scholar, linguist, entomologist and ornithologist, inventor of the famous "Berliner Blau" (a much-used blue dye), and proponent of a silk industry based on local mulberry plantations (Fig. 16). As a naturalist, he studied the life of animals "to praise the eternal Creator". He had gathered a wealth of experience on long journeys in Austria, Hungary, Italy, Switzerland, and Germany, before settling in Berlin in 1698 (Schalow 1919). Here he collected data on insects and the avian world specifically to support his physico-theological studies. He published the first book on the insects of Germany, *Beschreybung von allerley Insecten in Deutschland* [*Description of all kinds of insects in Germany*], in 1720–1738, and the first German bird book in 1733–1763, *Vorstellung der Vögel Deutschlandes und beyläufig einiger Fremden* [*Presentation of the birds of Germany, with some from other countries*]; Fig. 17.

The latter is a large folio work with 307 excellent colored illustrations of birds, as far as possible life-sized, on 256 copperplates, which were mostly engraved by Frisch's son Ferdinand Helfreich, 28 in the final year also by his grandson Johann Christoph, and hand-colored by F.H. Frisch and his wife. The natural colors lend the birds a very lifelike appearance. Where it was necessary and possible, male and female of a species are illustrated together, often one across the other. These plates became models for later bird artists because of their excellent color reproduction and positioning of the subjects. The original drawings for the engravings are today in the Stadtbibliothek Mainz (Schlenker 2004, 2005); Figs 18a, b.

Schalow (1919) and Stresemann (1941b) gave bibliographical details on the publication dates of the various installments over 30 years, but neither informed modern

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Fig. 16. Portrait of Johann Leonhard Frisch (from Schalow 1919).

ornithologists about the book's biological and historical significance. Schalow (1919: 522) wrote, without further explanation, "As far as the biological information set out in Frisch's work is concerned, I will not go into details here. It is based on Frisch's observations of birds in the field as well as of his own captive birds". Stresemann (1941b: 4) said, "regarding the scientific importance [of this work], I intend to return to the matter at a later date", which he never did.

Bastardization. Frisch was aware of the biological species criterion (successful sexual reproduction) introduced by John Ray, and already knew that certain closely-related species that would never hybridize in the wild could do so in captivity, but that the resulting crosses were sterile. He made the following interesting observations on hybrids and hybridization, under the title "On the Canary" (1733, end of Class I):

"Firstly: All bastards are from those species of animals that are closely related in many of their characters. Therefore Goldfinch and Canary, and all other birds of this first Class that produce bastards, must be closely related to each other. It is simply not possible with others; the Nightingale male can be as willing as he wishes, and the Canary female mate with many different birds, one cannot pair them or get them to mate because they are not very closely related. So donkey and horse, or dog and wolf, can have young together, but not horse and deer, or dog and bear.

Secondly: All bastards are born to animals that have been forced to come together, that in the freedom of nature would never mate with each other. […] A bird that cannot find another of the same species in one place flies to another part of the world to find one there.

Thirdly: All bastards resemble their fathers in the head and tail. The mule has its head and tail like a donkey, the

Fig. 17. Title page and frontispiece of Frisch (1733–1763), with an engraving of a memorial bust of J.L. Frisch and portrait of his son Ferdinand Helfreich Frisch by the naturalist's grandson Johann Christoph Frisch, from a design by B. Rode.

rest of its body like a horse. The bastard of a Goldfinch father shows the head and tail of its father and the body of its mother, the Canary.

Fourthly: All bastards are sterile. As is well known, the mule cannot reproduce, and this is also the case in birds. No young can be got from a bastard. The main reason is that the blessing at the Creation spoken over the animals, Be fruitful and multiply, does not apply to them. They have from their father and mother the blessing of life but not of multiplication. The inventions and restrictions of Man can create a third thing from two by mixing and the effect of nature, but it is not a new creature that can reproduce, only a temporary, deficient thing.

Fifthly: A special circumstance that is to be noted when breeding birds is how far the blessings of Creation extend. Birds are created to incubate their own eggs, an indispensable part of reproduction. If an alien bird incubates an egg then a half-bastard will hatch from it; that is, the bird that emerges is like the parents but will never itself reproduce. They can lay eggs, good fertile eggs, but do not in-

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cubate them. At the time when the eggs must be incubated they are incapable of doing so, and only because the eggs from which they hatched had been incubated by an alien bird. Many householders have experienced to their loss that ducks hatched from duck eggs incubated by a chicken are of no use for breeding. A certain gentleman wanted to have many pheasants on his land and his 'clever' managers had the pheasant eggs he had bought incubated by chickens; the pheasants that hatched did not procreate."

The idea of the "half-bastard", which seems so peculiar to us, was later picked up by J.H. Zorn as a partial explanation for the non-incubating Cuckoo (see below, and Haffer 2006: 52).

Frisch also observed that snipe are able to open only the tip of their long bill, while most of the bill itself remains closed. Kingfishers, which breed on the steep banks of the Oder river east of Berlin and which he kept in his aviaries, regurgitated "pills" composed of undigested fish bones and scales. By tying threads dyed with red watercolor to the feet of swallows he proved that they do not hibernate in the mud under water, as was then widely believed. When the birds returned next spring the threads had not lost their color. He concluded, "Most probably they fly to a country where they find food in wintertime".

Frisch divided the birds into 12 Classes:

"I. Small birds with short thick bills, for splitting hempseeds
II. Small birds with thin bills, for eating flies and worms
III. Thrushes and blackbirds
IV. Woodpeckers and 'tree hackers'
V. 'Jays' and magpies
VI. Ravens, crows, and jackdaws
VII. Diurnal birds of prey
VIII. Owls and night-birds
IX. Wild and domestic game-birds
X. Wild and domestic pigeons
XI. Wild and domestic geese and ducks and other swimming birds
XII. Birds that like to be close to water or swampy places."

Frisch's species names are listed in online Appendix 2. He had a good overview of the German avifauna, though un-

a

b

Figs 18a, b. Two plates from Frisch (1733–1763). 18a: male and female Golden Oriole; 18b: Common Redstart and European Robin (top), adult and first-year male Bluethroat.

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derstandably several reed warblers, *Sylvia* warblers, leaf warblers, geese, ducks, raptors, gulls, and waders were missing. In the following, we comment on several of Frisch's statements on a selection of species, and on some of the birds illustrated on his color plates (cf. also Haffer 2006: 49–51). We follow the numeration of his plates (see also the review of the birds of J.L. Frisch in Bechstein's *Handbuch* [Vögel 2, pp. 583–741, 1793] and in Schalow 1919: 51–61). Frisch also illustrated some exotic birds, which were in cages (parrots) or in the farmyard (Turkey, pheasants), as well as various varieties of the Canary and domestic pigeons and chickens, which we do not discuss here.

Dompfaff or *Blutfink [Bullfinch]*, Plate 2: "Three different species are found of different sizes. Whether this difference is the same everywhere, or varies from place to place depending on better or poorer feeding for the birds, must be further investigated." Frisch was probably familiar with the large race of the Bullfinch that appears in Germany as a winter visitor from northeastern Europe. On the other hand, Bechstein (p. 588) thought that the case here was one of individual variation and that Bullfinches varying greatly in size could be found in the same nest.

Gelbkehliger Hänfling [Twite], Plate 10, Fig. 1: Frisch writes of this bird, "This is the third species [of linnet-type birds] known in our region, but only to the bird-trappers, who strangle them along with other birds, otherwise it is unknown. In the Mark Brandenburg it is called '*Quitter*'. They appear in small numbers and are trapped at finch decoys; has no song that one can hear when it is in a cage, and leaves the area again in February."

Bechstein (1793: 483, 593–594) had no personal experience of the Twite ("I have never seen it [Arctic Finch, *F. flavirostris*] in Thüringen; but it has been observed in winter in Oberhessen") and believed that the bird illustrated here was a two-year-old Linnet, though he added, "Where this bird gets its yellow bill from I do not know; because as far as I am aware the Linnet in winter has a whitish, or whitish-yellow bill, but I have never seen one that was sulfur-yellow, as it is shown here."

Kreutzschnabel, Grünitz [Common Crossbill], Plate 11, Fig. 2: The text refers to this species, but the pair illustrated are surely Parrot Crossbills, as is evident from their large bills. Bechstein (*Handbuch*, 2nd edition 1807, p. 21, footnote) recognized that this was the case, and wrote," When one looks at the plate in Frisch, because of their size and the thickness of their bills, the birds shown there are certainly Parrot Crossbills. The writer must have been able to obtain this bird much more easily in the pine forests than the Common Crossbill. But when one reads the accompanying description, it does fit much better to Common Crossbill, so it has probably been copied from personal or written sources." In his text Frisch describes in great detail the feeding behavior of crossbills on conifer cones and their breeding in winter (see Haffer 2006: 50).

Brachlerche [Tawny Pipit], Plate 15, Fig. 2b: "When it sings, which it does to attract a female, it sits on a slightly higher post or tree, from which it sometimes flies high into the air so that it can be heard even farther away, but it soon returns to a perch again. […] It can be told from the Sky and Wood Larks by its wagging tail, while the Tree Pipit [*Gereut-Lerche*] is rather thinner and longer. But all of them are almost identical in color."

Wiesen-Lerche [Meadow Pipit], Plate 16, Fig. 1b: "….. climbs high into the air so that one cannot see it any more … There are very few of these larks and many bird-trappers do not know it. … It feeds in grassy places and meadows, and like the Sky Lark in young crops, and eats worms and other kinds of creeping vermin … It wags its tail just like the Tree Pipit]."

Bechstein, who initially regarded Tawny and Meadow Pipit as one species, wrote (*Handbuch*, 2nd edition, 1805, p. 302, footnote): "These birds, namely Tawny, Tree, and Meadow Pipit, have been the source of many errors in natural history publications. I myself have also been led astray. Therefore, since they differ markedly from the larks, I have created a new genus for these birds which I have called *Anthus*."

Schwarz-Kehlein [Common Redstart], male Plate 19, Fig. 1a; female and juveniles Plate 20, Figs. 1a, 2a, b: "This bird is by some people divided into Common Redstart [*Garten-Röthling*] and [*Stadt-Röthling*] depending on where it nests and sings. The latter sings very loudly from houses or roofs. […] The song begins as early as March so it is very pleasant to hear". It is possible that Frisch refers here to the Black Redstart, which colonized Central Europe during the 18th century from the south.

Blaukehlein [Bluethroat], Plate 19, Fig. 2a, b; Plate 20, Fig. 1b: Frisch described the female on Plate 20 as a *Rothschwänzlein* with a half-red, half-black tail, clearly not recognizing the bird as a Bluethroat.

Two kinds of Nightingale [Common Nightingale and *Thrush Nightingale* or *Sprosser]*, Plate 21, Fig. 1: "Two species have been separated, since one is slightly redder than the other and is called *Rothvogel* ['Redbird'], while the other, called by some *Sproßvogel* or *Sprosser*, is slightly bigger and has less red on the tail. This Sprosser sings more at night than the other one. In the song itself there is very little difference between the two. A musician could perhaps describe the keys of this song, since it is not possible to even guess at the way it is done from the movements in the neck and throat of these birds. If one could measure the strength of the sound made by a Nightingale

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one would have to be amazed that such small lungs could produce so much air." Further there are detailed instructions how to keep and feed these birds in a cage.
Mönch mit schwarzer und mit röthlicher Platte [Blackcap], Plate 23, Fig. 1a,b: Frisch, just as the later J.H. Zorn (1743), took male and female Blackcap for two different species.

Weidenzeisig [Chiffchaff], Plate 24, Fig. 1: The bird illustrated is of this species; Bechstein (1793) thought that it was a Willow Warbler.

Blauköpfige rothe Amsel [Rock Thrush], Plate 32, Fig. 2: "This bird is known only in a few states in Germany. … [This illustration] was sent to me from Dresden by a good friend, under the name of *der grosse Roth-Wüstlich*. … It breeds or nests in the highest buildings in the scaffolding holes". Bechstein (1793: 615) commented on this peculiar statement as follows: "What Frisch says about these birds whose illustration he received from Dresden, that they nest on the highest buildings in the scaffolding holes, and that they have a song that is part high, pure whistling and part very similar to the song of the *große Grasmücke*, sounds very much like the Wistling (*Motacilla Erithacus* L. [= Black Redstart]), which also resembles these birds in that it is bluish on the upperparts and has a rust-colored tail." Clearly only the illustration of this caged bird came from Dresden, while the bird itself was possibly trapped in the hills to the south of the city.

Rabe [Common Raven], Plate 63: The text refers to the Common Raven but the bird on the plate is a Carrion Crow, which Frisch (in eastern Germany) would not know as a breeding species. Bechstein (1793) too had his suspicions, commenting on the illustration, "If one did not know that this is meant to be a Raven, one would think it was a Carrion Crow (*Corvus Corone* Lin.)".

Grau-weisser Geyer or Falck [Hen Harrier?], Plate 79: "It is not common in our region, but it is native … also pulls grasshoppers to pieces." The bird shown on the plate shows no black patches on the secondaries. Bechstein (1791: 256) described the Blauer Habicht (*Falco cyaneus* = Hen Harrier) as a good species, but later, in 1793 (while reviewing Frisch's birds), he summed it up as being inseparable from the Halbweye (= Montagu's Harrier).

Weisser Geyer or Falck [Pallid Harrier?], Plate 80: "Rather smaller than the previous species, the foot to the knee not so long. The wing feathers are edged brownish yellow in the previous species, in this one edged white. The inner primaries in this species are pale gray, in the previous one black."

Rothes Italiänisches Rebhuhn [Red-legged Partridge], Plate 116: But the illustrated species is, given the narrow flank banding, black bib border, and well-defined breast band, a Rock Partridge (*Alectoris graeca*).

Wilde Gans [Greylag Goose], Plate 155: "In reality this is the well-known and everywhere common wild goose, also called Grey Goose." The bird in the illustration is, however, a Bean Goose, shown by the orange-colored patch on the upper mandible.

Moppelgans [Red-breasted Goose], Plate 157 Suppl.: "The actual India, or part of that country, in which this goose is resident or nests, remains unknown to us."

Nordische schwarze Ente [Velvet Scoter]: Plate 165 Suppl.: "It actually inhabits the coasts of Norway, but often crosses the Baltic, especially in winter, to the coast of Prussia. The whole body is velvet black with silky soft feathers; the male has a fleshy knob over the base of the bill, which the female lacks. The stomach is often full of snail shells."

Grosse Halb-Ente [= Black-throated Diver/Arctic Loon], Plate 185, Suppl.: "As big as a goose; it can weigh up to 32 pounds … When this bird lays eggs it screams as horribly as a man in fear of his life calling for help." Because of the powerful bill, the species illustrated is not a Black-throated Diver but a Great Northern Diver/Common Loon.

Bienenfresser [European Bee-eater], Plate 222: The origin of the bird in the plate is not the Mark Brandenburg but East Prussia, since J.T. Klein (1760, p. 113) in Danzig wrote, "I have sent a nice illustration in lifelike colors to Frisch in Berlin, which he used to produce the bird on Plate 222, and from which one can best see the beautiful colors".

The physico-theologian Johann Heinrich Zorn and his handbook of ornithology (1742–1743). The Protestant pastor Zorn (1698–1748) wrote a two-volume handbook on the general and specific ornithology of southern Germany with the title *Petino-Theologie*[2] (1742, 1743), with which, within the framework of natural theology, he desired to make "*An attempt to encourage men, through closer observation of birds, in the admiration, love and reverence of their most powerful, wise, and benevolent Creator*", thus the subtitle of his work (see online Appendix 2). The foreword to the second volume contains the guiding principle of physico-theology: "God's existence and qualities can be deduced from the nature of every creature" (p. 5). In the first volume, which deals with general ornithology, the author discusses the functional anatomy of birds as well as molt, behavior, reproduction, movements and migration (see Haffer 2006: 18–20). In the second, in over 250 pages he reviews the ca. 130 species oc-

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curring in the mid-Franken region where he made his observations. Given the lack of large water bodies there, many wetland and water species are missing. It was not Zorn's intention to compile an exhaustive avifauna of southern Germany, but as a physico-theologian it was rather his aim to describe the wonderful adaptations of birds to "encourage men in the reverence of their Creator". For every species Zorn described (in varying detail) plumage color, nest site, breeding, the rearing of the young, feeding, behavior, song, occurrence, and migration. He possessed considerable field experience gained over many years of observing in the wild. The *Petino-Theologie* is not illustrated. Zorn had hoped to publish color plates in several supplementary installments but died in 1748 before he could complete the work.

He classified the birds as follows:

I. Landbirds
Birds of prey, some of which hunt during the day and some at night
Ravens, crows, jackdaws, and magpies
'Jays'
Woodpeckers
Game-birds and larks
Pigeons and doves
Landbirds
Thrushes, blackbirds, and Starling
Seed-eating birds
Worm- and insect-eating birds

II. Waterbirds, some of which live on the water, and are called swimming birds; some of which live by the water, or in wet and marshy places, and are called marsh- or bog-birds

In Volume 2 of his *Petino-Theologie* (1743), Zorn makes brief pertinent comments on every species regarding appearance, behavior, and occurrence. We quote here, in the order in which the species are listed, selected statements that are of interest for a variety of reasons:

Gelbe Bachstelze [Grey Wagtail], p. 94: "Likes to build its nest in water ditches, by watermills, and in old walls."

Guguck [Common Cuckoo], p. 245: "Since I am of the opinion that this bird sucks the eggs of other birds and leaves the empty shells in their nests, I have put it in this class [birds of prey]." Zorn knew a great deal about the brood parasitism of the Cuckoo, and postulated that the young Cuckoo forces the host nestlings out of the nest (Haffer 2006: 51–53).

Der mittlere Neuntödter [Woodchat Shrike], p. 251: "The whole back of its head is colored light brown or brick-red, which continues over the short neck down to the back. This meets a black mantle bordered reddish; on both sides are white patches against the black."

Birkheher [European Roller], p. 268: The bird is now and then seen here in pairs "which nest in holes in hollow oak trees and have three, sometimes four young".

Blau-Specht or *Kleiber [Eurasian Nuthatch]*, p. 274: "When the hole in which it wants to nest is too wide, it plasters it with clay so it is then just wide enough for it to creep in and out." Stays here in winter.

Feldlerche [Sky Lark], pp. 291–292: "The extended secondary feathers near the body cover the wings proper, so keeping them dry when in wet grass, as well as protecting them from wear."

Gereuth-Lerche [Tree Pipit], p. 297: Pernau "wants this [species] in the wagtails rather than in the larks, because it always wags its tail; but the colors, feet, occurrence, the song, and the way it is executed, all combine to prevent this bird being considered as anything but a lark."

Brach- or *Koth-Lerche [Tawny Pipit]*, p. 298: "The author of *Agreeable country pleasures* [= Pernau], p. 99, wants to count this species too among the wagtails and, to distinguish it from the others, give it the name Field Wagtail; but the characteristics already mentioned should suffice to make it clear that the bird belongs to the larks."

Pip-Lerche [Meadow Pipit], p. 299: "The much praised Herr Frisch writes of this bird: It breeds in bare places, especially in meadows where people do not go much, and makes its nest sometimes under a clod of turf or earth; from the way it makes its nest it is called the clay bird."

Amsel [Blackbird], pp. 318–319: " It likes to be near water, wells, and rivers where it finds food. In spring it has its young before any other woodland birds, in early March."

Gold-Amsel [Golden Oriole], p. 322: "Its nest is hung like a basket on the fork of narrow branches."

Gemeiner Fink [Chaffinch], pp. 331-332: The spring plumage of the male is not created by molt. "The old feathers do not fall out, as stated in *Country pleasures* [= Pernau]; they just change color." "As well as [grain and seeds] it eats all kinds of flying and crawling insects, with which it also feeds its young from the bill."

For *Stieglitz [Goldfinch]* and *Grünfink [Greenfinch]* Zorn stresses that the nestlings are fed from the crop.

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Kreuzschnabel [Common Crossbill], p. 346: When the fir crop is good this visitor breeds in winter, "as Herr Frisch has also remarked on".

Goldammer, Emmerling [Yellowhammer], p. 347: The bill "has something unusual: it is short but pointed towards the tip, the lower mandible has an indentation on each side, while the upper has a bulge on each side which fits into the indentation, so that the bird is able to squeeze the grains of barley and other cereals it feeds on out of their husks, and other seeds are peeled." The nestlings are fed with "all sorts of larvae and worms and flying vermin".

Platten-Meise, Nonn-Meise [Marsh Tit], p. 364: "They hide hemp seeds in the bark of trees, or between the branches, so they can live off them at a later time."

Wiedhopf [Hoopoe], p. 368: "The nestlings stink, which comes from the excrement that the parents do not remove from the nest."

Mönch mit schwarzer Platte [Blackcap], p. 373: "I have long been in doubt about whether the female of this bird also has a cap or not; but I had some shot in the spring of 1741 and there were ones with black caps that had testes and some that had ovaries, and the only difference I could see was that the female cap was not so black as the male's; they are also slimmer than the males, which are fatter and of a darker color."

Mönch mit der röthlich- oder braunen Platte [Blackcap], p. 374: "That this is the appearance of the male of this [species] of warbler cannot be doubted by anyone who knows about birds. Its clear and loud song, which one can watch and hear it deliver in the spring in places where trees have been felled, settles the question. However, what the female looks like I have been unable to learn from anyone who has written about these birds. Even the sharp-eyed Herr Frisch is uncertain on the matter. He writes: Some say the red-capped one is the juvenile of the black-capped; but it is a male, his female is exactly the same color and has no trace of red". Both Frisch and Zorn, despite intensive researches, thought that there were male and female black-capped warblers and male and female red-capped warblers.

Dornreich with song-flight *[Common Whitethroat]*, p. 377

Kleiner Steinschmätzer [Whinchat], p. 381: Frisch included this species in the *Grasmücken* [*Sylvia* warblers], Pernau in the redstarts': " But I do not see on what grounds. For it is very different from the redstarts. It is speckled, has no red tail, breeds on the ground, in hedges, under rocks and clumps of earth, while the redstart nests in holes in trees or in walls. I include it therefore in the wheatears, because it has almost the same call and song as the large Wheatear, prefers to be among hills and rocks, and nests under or against stones."

Hauß-Schmätzer [Spotted Flycatcher], p. 382: "Moves tail and wings at the same time when it is standing, letting the wings hang. Has no song, male and female look very similar."

Schwarz und weiß-scheckigter schmätzender Fliegen-Vogel [Collared Flycatcher], p. 383: "The bill of the male is coal-black; above it he has a snow-white patch, then above that over the head down to the nape is coal-black, extending to the sides of the face. Below the nape there is a white ring around the neck. The bird is coal-black again on the back, except the rump, which has a white patch adjoining the black tail-feathers." In his home region, Zorn possibly only saw Collared Flycatcher, with its "white ring around the neck".

Hauß-Röthling [Black Redstart], p. 386: This species was already widespread in mid-Franken in Zorn's time.

Hauß-Schwalbe [Barn Swallow], pp. 398–399: The Barn Swallow, with long tail feathers, builds a flat open nest and can sit on it without damaging these feathers. House and Sand Martins breed in holes and have no long forked tail! "A special providence of the Great Lord."

Wilder Schwan [Whooper Swan], pp. 403–404: In the cold winter of 1740 around 30 individuals "made a loud din calling in flight that one could hear at a great distance. The front of the bill is coal-black, then yellow towards the head, the yellow continuing onto the skin of the front of the head"; without a knob at the forehead.

Mergente [Smew], p. 412: Head brown; the female.

(4.) Standstill in research (1750–1788)

From around 1750 until the end of the 1780s no important works appeared containing new findings in avian biology in Central Europe. The books by J.T. Klein (1750, 1760) simply contain lists of the bird species in Europe and elsewhere, as far as they were known (see below). Two loose-leaf collections of birds (B. Dietzsch, *Collection of mostly German birds*, 1772–1782) and of their nests and eggs (F.C. Günther, *Collection of nests and eggs of different birds*, 1771–1786) appeared, containing respectively 101 and 108 colored plates. The bird plates are considerably poorer than those in the earlier excellent work of Frisch (1733–1763), and only about half of the plates in both works are accompanied by short texts (see Haffer 2007a for further details and later literature).

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The field ornithologist W.H. Kramer (1756) distinguished Common Nightingale and Thrush Nightingale or Sprosser, and reported on other species in his avifauna of Lower Austria. The Benedictine friar Leopold Vogl (1785; see Feldner 2002) made interesting observations on nest building, breeding, and behavior of the Siskin (*Carduelis spinus*). The translation by B.C. Otto of Buffon's *Natural History of Birds* which appeared in 35 volumes between 1772 and 1809 – the first six volumes had been translated by F.H.W. Martini – was important in as much as Otto inserted his own observations on the occurrence and distribution of many species in northern Germany (Wenzel 1909). Now and again he referred to the "old experienced Zorn". These volumes of Buffon's work found a large public in Central Europe.

However, in the last two decades of this period of time those researchers whose publications from 1789 onwards would usher in the flowering of Central European field ornithology began to be active: Johann Andreas Naumann, followed by his son Johann Friedrich, and Johann Matthäus Bechstein.

A compiler – Jacob Theodor Klein (1750, 1760). This first ornithologist in East Prussia was the town clerk of Danzig and lived from 1685 to 1759. He possessed a famous natural history collection, containing plants, animals, minerals, and ores, which in 1740 was transferred to Bayreuth and subsequently to the Zoological Institute of the University of Erlangen. Following Carl Linnaeus, he set out to classify several animal groups solely on the basis of their external characters (Geus 1970), including the birds (Klein 1750, 1760). These classification attempts are placed ahead of the species lists in his books. Although Klein's works are often cited in the literature, they are little more than compilations (including some extra-European species) containing no fresh data. They are lists of names with brief inadequate descriptions and hardly any biological information on the individual species. Since for many Central European species Klein gave the number of the color plate that depicts them in Frisch (1733–1763), we were able to compare his German names with their present-day equivalents. A collation of Klein's list with the Linnaean names in Beckmann-Reyger (1774) resulted in complete agreement. Beckmann's list however is far from comprehensive, leaving the identity of many of Klein's bird names uncertain. Klein dealt with a total of 213 Central European bird species, a similar number therefore as Frisch, though less than Bechstein or Naumann because he had omitted some raptors, wetland species, gulls, Middle Spotted Woodpecker, some pipits, reed warblers, and leaf warblers (online Appendix 2). Some of his wetland birds, ducks, and gulls cannot be identified. The notes to some species are quoted here verbatim because of their historic interest:

Trieltrappe [Little Bustard]: "In the year 1737 a hen was shot and brought to me, and being so beautiful I had her drawn […] she was close to laying and had 2 eggs inside her."

Gehörntes Käutzlein [Long-eared Owl]: Klein says "In size the same as a wild pigeon", i.e. ca. 32–37 cm; Scops Owl measures only 19–20 cm.

Blauköpfige rothe Drossel and *Blaukehlein mit rother Brust [Rock Thrush]*: "The neck, the throat, and head are cornflower-colored, the back shades into black, […] belly and tail are reddish. It lives among rocks and is not so common in our area; but in 1756 I received a pair from Oliva, and 3 birds were sent to me from Bordeaux."

Parisvogel [Pine Grossbeak]: "It also comes to us in Preußen: They are not seen in our region every year, only sometimes."

Klein's natural history cabinet also held a collection of good color plates of European and exotic birds made by various male and female artists during 1655 to 1737, which can still be seen in Erlangen (Braun 1906, 1908; Gengler 1912–1913). See Schöndorf (2008) for an account of "the first German bird collection in the west", that of Jean Holandre in Schloss Karlsberg in the Pflalz, and also Holandre (1785).

(5.) The flourishing of field ornithology around 1800

The widespread practices of fowling or bird-trapping, at a "fowling floor" (*Vogelherd*) or decoy, and keeping birds in cages and aviaries led J.A. Naumann (1789), J.M. Bechstein (1791–1795, 1805–1809), and J.A. & J.F. Naumann (1795–1803, with supplements 1804–1817) to collect the knowledge they had gained through practical experience and observations of individual species in the wild in good ornithological handbooks. In so doing they initiated the flourishing of field ornithology in Central Europe.

Johann Andreas Naumann (1744–1826). "Old" Naumann (Fig. 19) was the owner of an estate in Ziebigk near Köthen, in today's Bundesland of Sachsen-Anhalt. He, and his eldest son Johann Friedrich (1780–1857) after him, were well-placed economically. They could easily afford the purchase of equipment, guns, and books and, importantly, also had the necessary free time for their ornithological activities (Wenzel 1988). Around 1774, when he was about 30 years old, Naumann senior wrote the manuscript for his first book *Der Vogelsteller* [*The bird-trapper*] (1789), but he only had it published, with additions, 15 years later (Baege 1980: 10). This was followed by his

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little book *Der philosophische Bauer* [*The philosophical farmer*] (1791), and soon after that the printing of his handbook *Beschreibung aller Wald-, Feld- und Wasservögel* [*Description of all forest, field, and water birds*] (1795 ff) began. Here we wish to discuss the ornithological content of *Der Vogelsteller* in some detail because this work has been neglected until now, although it heralded the flowering of field ornithology in Central Europe and hence is of particular historical significance; see Fig. 20.

Der Vogelsteller
oder die Kunst allerley Arten von Vögeln sowohl ohne als auch auf dem Vogelheerd bequem und in Menge zu fangen nebst den dahin gehörigen Kupfern und einer Naturgeschichte der bekannten und neuentdeckten Vögel. Leipzig, 1789

[***The Bird-Trapper***
or the art of trapping all kinds of birds, without as well as on a trapping ground, easily and in large numbers, with accompanying copperplates and a natural history of the known and newly discovered birds. Leipzig, 1789].

In this little book (18 x 10.5 cm) Naumann brought together the practical knowledge and ornithological experience he had gathered over several decades as an enthu-

Fig. 19. Portrait of Johann Andreas Naumann (from Thomsen & Stresemann 1957).

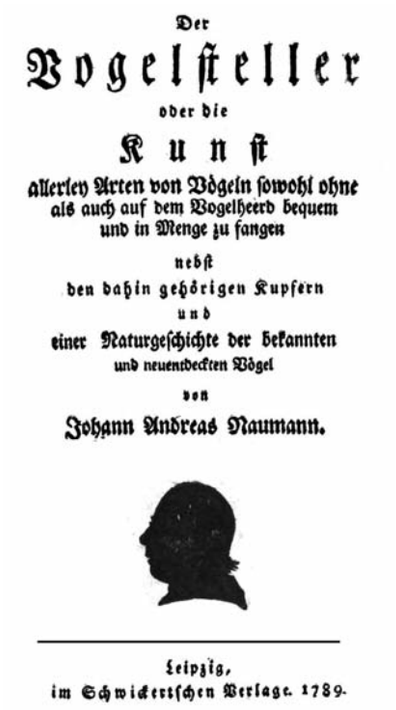
Der
Vogelſteller
oder die
Kunſt
allerley Arten von Vögeln ſowohl ohne
als auch auf dem Vogelheerd bequem
und in Menge zu fangen
nebſt
den dahin gehörigen Kupfern
und
einer Naturgeſchichte der bekannten
und neuentdeckten Vögel
von
Johann Andreas Naumann.
Leipzig,
im Schwickertſchen Verlage. 1789.

Fig. 20. Title page of J.A. Naumann (1789).

siastic bird-catcher and watcher. The first edition appeared in 1789, it was later reprinted (1806) and then sold with differing title pages (Schlenker 1984). Although the book was republished with an epilogue by Baege in 1980, until now its ornithological content has hardly been given due attention. See online Appendix 3.

In the 1980s, in the Naumann Museum in Köthen, Ludwig Baege discovered a manuscript written by J.A. Naumann in his old age, and already known about from remarks made by his son Johann Friedrich. This manuscript, which was basically a continuation of *Der Vogelsteller*, was published in printed form (1989) by J. Neumann after Baege's death. In this booklet, Naumann discusses additional trapping methods and the experiences he had made with them after 1790, or had heard from others, but it contains no new ornithological findings.

The content of *Der Vogelsteller* is little known due to the rarity of the original, and also because bird-trapping for private or commercial purposes fell out of favor in the 19th century. Only Sunkel (1927), in his book on bird-catching, provides some extracts from Naumann's work. When a copy of the first edition of *Der Vogelsteller* was presented to one of us (J.H.) by Frau Amélie Koehler (Freiburg) – who in turn had received it as a gift from the library of Frau Vesta Stresemann – we were surprised to read at the end of the long title "……. *und einer Naturgeschichte der bekannten und neuentdeckten Vögel*" [……*and a natural history of the known and newly dis-*

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covered birds]. Never have Naumann's observations of individual bird species in *Der Vogelsteller* been described by a later author, let alone commented on or analyzed. We wish to make up for that omission in the following pages, since Naumann's are the first, and extremely interesting remarks on the natural history of Central European birds since the appearance of J.L. Frisch's folio work (1733–1763) and the two-volume *Petinotheologie* of J.H. Zorn (1742, 1743), two publications Naumann did not mention and almost certainly did not know. He probably did not possess B.C. Otto's German translation of Buffon's great work either, in which Otto had inserted many comments on north-German birds. Both Frisch's book and the Buffon translation found their way into Naumann's library later, and father and son quoted extensively from them, as well as from other ornithological literature of their time; see Hildebrandt (2007: 10).

At the end of *Der Vogelsteller*, Naumann introduces himself to the reader in a comic dialogue between a House Sparrow and a Tree Sparrow, the former saying of itself, "my landlord is a good man, he is a bird lover and allows me much freedom; while he sometimes punishes my too great cheekiness he does so with moderation and within the rules; my landlord has more pleasant things to do [than pepper me with his gun],

Denn er hat Acker, Drescherklang.
Garten, Busch und Vogelfang,
Wiesen, Jagd und Fischerey.
Da lebt er vergnügt dabey,
Schlägt oft fröhlich in die Hände,
Und wünscht sich dieß bis an sein Ende."[3]

[For he has fields, the sound of threshing, garden, woods, and bird-catching, meadows, hunting and angling. With all this he lives happily, claps his hands for joy, and hopes it will never end until his dying day.]

The text of Naumann's little book, following a foreword (pp. III–VI) and an introduction (pp. 1–6), is subdivided ornithologically and not on the basis of the various trapping methods, like nets, decoys, etc.:

I. On the trapping ground and the birds that can be caught there (pp. 7–132)
II. On other woodland birds, their food, feeding, and trapping (pp. 133–161)
III. On birds of prey (pp. 162–173)
IV. On field birds (pp. 174–184)
V. On waterbirds (pp. 185–199)
VI. On tame birds (pp. 200–206)

Two copperplate engravings at the end of the book illustrate a trapping ground or fowling floor, as well as snares, nooses, and other bird traps.

Foreword. In his "Foreword to the bird-trapper" the author stresses that during the migration period one must look after the trapping ground carefully and daily, even when one has caught no birds for days. Wind and weather can suddenly turn favorable for migration and a large number of birds could arrive at any moment. The trapper should be able to recognize the different species and know their calls and way of flying: "the sweet joy that one experiences from the knowledge gained will never allow its fire to be extinguished" (p. V). Most of the fowlers at that time judged the birds they had caught solely on the taste of their meat or on their value on the market. By contrast, Naumann's interest in the differences between the various species and in their lives, their "natural history", meant a considerable step in the flourishing of ornithology in Central Europe (Baege 1980: 11).

Introduction. Hunting is a favorite pastime for very many people: "But if everyone who loves the hunt and sporting pursuits were allowed to enjoy them it would not be long until all game and birds were completely extirpated, therefore it is only natural that the upper classes have reserved the right to these excellent pastimes to themselves and that certain restrictions are imposed on their subjects" (p. 2). However, Naumann continues, in most places bird-trapping is a free activity, or at least can be carried out for a small fee. He wrote his little book on bird-catching to pass on the things he had learned to those who were interested. He had been a lover of this craft since his early youth, and came from a long line of fowlers. He introduced new techniques and discoveries into the subject, was grateful to learn new ideas from other trappers, and soon was very proficient in the art. In order that others might profit from his knowledge he put pen to paper, and everything he wrote about was based on his own experience.

Main text. Here Naumann discusses the individual bird species, with details of their colors and behavior, and has arranged them in an "ecological" order of his own (woodland birds, birds of prey, field birds, and waterbirds), communicating also much biological information. Many fowlers of the time knew a tremendous amount about the birds they caught and probably had no trouble following Naumann's explanations, even without illustrations. What interests us today is not only the wealth of detailed knowledge Naumann had of individual bird species but also the quality of his excursions into general ornithological subjects, such as territory occupation, sexual dimorphism, migration, song-supression – the holding-back or stopping of song in decoy birds until autumn. In those early days of field ornithology in Central Europe some bird groups still presented difficulties when it came to distinguishing between and identifying species. These broad topics are dealt with first, before the discussion of single species. Our additions to Naumann's text are in square brackets.

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General ornithological themes

Territory occupation in birds. "As soon as the Chaffinch [in the spring] sings loudly he has staked his claim, and tolerates no other finch in his territory" (p. 58). For Naumann, the territoriality of numerous species was self-evident. Since Aristotle described eagles holding territories, the occupation of territory has been rediscovered independently by many ornithologists (Pernau and Altum in Germany, Howard and Lack in England; see Birkhead 2008).

Sexual dimorphism. "It must be additionally noted that the male of many birds looks much more beautiful than the female, while in others the sexes can be differentiated only by being a little lighter or darker, which can hardly be seen even by an expert, and in others again the colors are very different, and where this is the case I have described the colors of both sexes" (p. 59).

Bird migration and winter quarters of Central European species. Migration is a well-known phenomenon, writes Naumann, and each group of birds seeks its way after its own fashion: "As a sailor on the sea finds his route with the help of a compass, so a bird finds its route again in the air by following its nature from one year to another" (p. 11). Naumann thinks that migrants leave their breeding grounds mainly because of the scarcity of their food in the autumn, not because of an innate instinct. In some places unusual weather conditions can bring alien birds, which are regarded as a sign of bad luck (p. 16).

The Nightjar "is a summer visitor, and as soon as it finds no more flies it moves elsewhere. All these birds, like the Cuckoo, Golden Oriole, Hoopoe, Dunnock, Nightingale, reed warbler, Barred Warbler [*and/or*] Lesser Whitethroat, Icterine Warbler, Willow Warbler, Robin, Common Redstart, Goldfinch, Whinchat, Tree Pipit, wagtail, and Wren move at night when it is still, partly because they are safe then from raptors and partly because the wind usually does not blow strongly at night, since these birds are not strong fliers" (p. 155). "All the birds that cannot find their food in the winter in our region migrate to warmer countries, since a bird that feeds on insects will find none in the winter and so must naturally move to a country where it can find such food. For this it does not require a long period of time for a bird can comfortably fly four or five miles in an hour. So if the wise Creator has made this part of the nature of all birds, I don't know why He should not have given this ability to the Swallow instead of, as many claim, changing them into something else, or causing them to bury themselves in swamps or hollow trees? Who will extract them from these places, and dry them off so that they can return to their life?" (p. 156). Naumann rejects the widespread belief that swallows overwinter in the mud of lakes.

Song-suppression. Naumann mentions the suppression of song several times ("Gesang-Verhaltung"; Aitinger 1626, 1653: 167) when writing about the decoy birds or lures on the trapping ground, without explaining this practice, which once was widespread and known to fowlers for centuries. "Suppressed birds are those that sing at a time of year that is different than the normal time for singing, and which are very useful in the autumn for attracting and catching wild birds" (Riedel 1833: 70, footnote).

"Many bird-catchers keep their Chaffinches all summer in a dark place so that they will sing when desired in autumn or winter, since as soon as they come into the light again they start to sing but do not sing in the dark, and they are used to lure other birds into the net" (Gessner 1555; see also 1669: 120–122).

"As soon as the bird which one wishes to suppress starts to sing, or just before this happens, it is put in a cage and, when it has found its food and water containers, the place where the cage is kept, perhaps in a box, is gradually made darker and darker until it is completely blacked out. The bird should be kept cool but comfortable and clean. Some keepers pluck out feathers at this time so that an artificial molt will prevent singing. Once the bird is in complete darkness, and knows where its food is, it should remain there until it is needed. However, at least four weeks before it is to be used it should gradually be reintroduced to the light and fed well, then it will let its song be heard" (Riedel 1833: 70–71).

"Regarding Chaffinches, Bulliard [1778] advises catching birds of the year in September or October to keep them as decoy birds for the start of the following spring. Then those that are best at luring wild birds are selected. So that they will sing in the coming autumn, when they will be most needed as decoys, one must deceive them as to which season it is, which the bird-trappers call suppressing or stopping (*Verhalten*). For this purpose, at the beginning of June the decoy birds are put into a cool room or cellar, and their cages made gradually darker and darker until they are in total darkness. A cage must then not be moved because the birds will be accustomed to finding their food and water at a particular place. An even better procedure was to let them feed every day in artificial light, and to pluck out some tail or wing feathers to create a 'forced molt'. At the end of September they were slowly accustomed to daylight, and then would fulfill their role as singing decoy birds in October" (Sunkel 1927: 234).

Therefore the fowler accelerated the annual cycle of the caged decoy birds by bringing them relatively rapidly through an artificial autumn, with molt, in early summer, from which they emerged between August and October singing their spring song. As stated above, fowlers had been using this technique of song-suppression for centuries. Birkhead (2008) and Birkhead & van Balen (2008) mention early reports on this by Conrad Gessner (1555), Manzini (1575), Aldrovandi (1599), and Aitinger (1626),

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and discuss the connection between suppression (or stopping) of song in cage birds and the avian annual cycle.

J.A. Naumann's remarks on song-suppression in decoy birds and the advantages of suppressed decoys during autumn bird-trapping are as follows:

"The song must do most of the work, because for them [the migrating conspecifics] it is something unusual at this time of year so they enjoy listening to it and swoop down eagerly to the trapping ground, hence a bird-catcher must above all ensure that he gets excellent singers" (p. 59). "When one [in the spring] has about eight of them [Chaffinches in cages] then they are hung outside at a window, and after they have sung loudly for a few days, and no longer stammer, they are brought in and put in a dark closet or box until St. Bartholomew's Day [= August 24th], when they are taken out and hung up again outside. Those birds that start to sing again inside a few weeks are good ones, and those that do not sing can be rejected and replaced by others after their time outside" (p. 60). "A good Chaffinch will start his song in March or April, but those that start singing at the end of May, or even around St. John's Day [= June 24th] are of no use because they will very rarely pick up their song again in autumn" (p. 63). According to Naumann, blinded birds sing much better than sighted ones because nothing disturbs them. "If one wishes, one can put a good male [Yellowhammer] […], as with the Chaffinches, in a dark closet, so that he keeps his song until autumn, then one will attract far more wild birds at the trapping ground" (p. 71). "The decoy birds [of the Ortolan] are kept in darkness, just like the Chaffinches, in order that their song is retained because without good song nothing much will be achieved [in the autumn]" (pp. 73–74).

Species knowledge. The list of species dealt with is restricted to the birds which Naumann observed in the immediate vicinity of his place of residence in northern central Germany. This is the reason why there are gaps in the wetland species (swans, geese, herons, ducks, gulls, waders) and in some of the songbird groups (reed warblers, leaf warblers, *Regulus* sp., treecreepers). However he filled many of these gaps in later years.

Trapping methods

Trapping devices like the fowling floor and its lures, nets, nooses, and cages are discussed at length in Part 1 of *Der Vogelsteller*. A trapping ground must be erected in a favorable place, with singing birds and decoys. When setting up a trapping ground one must "know the thoughts of the birds, if I may so express myself, so that one erects everything just the way the birds like to have it" (p. 10), that is, the fowler must know their habitat schema. The main point is to " abolish everything of artful appearance that to our eyes appears beautiful, and to arrange the trapping ground so that in the eyes of the birds it seems natural and attractive" (pp. 42–43). One catches few birds in strong winds or in mist; the best kind of weather is overcast and still. Advice on the keeping of decoy birds follows, and on the best type, size, and fittings for a bird cage, as well as on the various kinds of food. Naumann also discusses nets and traps for different bird species (pp. 48–57).

On the different kinds of trapping grounds or fowling floors (pp. 91–111): An area for catching Chaffinches (*Finkenherd*) must have a covering of thick grass as well as trees around the trapping ground, for the wild birds to alight on, and from which to hang the decoy-bird cages. Naumann goes on to describe many additional contrivances on the trapping ground for other decoy birds, such as the "runners" (*Läufer*), which are kept on the ground by having their wings tied to their bodies. On a "shrubby trapping ground" (*Strauchherd*) the grass in an open area with shrubs is cut evenly using a sickle, the grass below the shrubs is removed, and the soil swept clean. Twigs of rowan berries are stuck in the ground beneath these shrubs as well as attached to them, the more the better. The bird-trapper transports his nets and cages only on long poles. He watches the trapping ground from a hut and observes how many birds arrive. From the courtship calls of his lures he must be able to recognize whether the wild birds are near or far, and to distinguish courtship calls from warning calls. He must be especially on the look-out for weasels and birds of prey, which can easily kill the decoy birds.

On snares (springes) and nooses (pp. 111–122): A wide range of trapping devices, many of which Naumann himself improved, are decribed in great detail and with illustrations.

I. On the trapping ground and the birds that can be caught there (pp. 7–132)

In each species section, before his general and biological remarks, Naumann provided a brief description of plumage, which we have omitted here.

Fink [Chaffinch] (pp. 58–64): The bird-trappers distinguish between different classes according to their song (*Schitzkebier, Deutschebier, Reitzu, Nutschkebier* and *small Schitzkebier*) [these fantasy names are onomatopoeically based on the various songs], and then there is the *Waldgesang* [woodland song], which cannot be compared with them. "Bird-catchers are of differing opinions concerning the song. Some say that the *small Schitzkebier* is most suitable for attracting wild birds, others praise the *Reitzu*; personally I believe that the best song is the one that is the commonest among the Chaffinches" (p. 64).

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Quäcker [Brambling] (pp. 64–66): After the Chaffinch this is the most important bird on the trapping ground. "Where it nests I cannot say, because I have never seen a Brambling in the breeding season in our region" (p. 64). Young cocks make the best decoy birds.

Schwunsch [Greenfinch] (pp. 66–68): Migrates with the Chaffinches into December, but singly. It particularly likes hemp seeds.

Zeisig [Siskin] (p. 68): "The smallest bird among those that are caught on the trapping ground, but it tastes the best. […] They hang continually on the fruits of alders and eat their seeds."

Schättgen or *Schittscherlingen [Redpoll]* (p. 69): "The character and qualities of the Redpoll are exactly the same as those of the Siskin. They are always together with them." They are rare, though singles are seen almost every year, and in some years they are very common.

Stieglitz or *Distelfink [Goldfinch]* (pp. 69–70): A well-known bird, which however is only caught as singletons.

Hänfling and *Steinhänfling [Linnet* and *Twite]* (p. 70): There are (a) the large red-breasted Linnets and (b) the small Twites, and both of them are only caught singly and with some trouble. They are frequently seen in quite large flocks on the stubble fields in winter.

Grünschling or *Gehling [Yellowhammer]* (p. 71): Another well-known bird that is caught as singletons.

Strumpfweber [Corn Bunting] (pp. 71–72): "They get their name from their song, which sounds like a stocking-weaver working at his loom." They move away in September but many remain here all winter.

Schiebge or *Rohrammer [Reed Bunting]* (pp. 72–73): Lives in bushy places where it is marshy and where there is plenty reed, whose seeds and those of other grasses it feeds on. "It does not breed in our region." Their main movement is in October. Reed Bunting, Yellowhammer, Corn Bunting and Ortolan are closely related to each other.

Ortolan [Ortolan Bunting] (pp. 73–74): "Where this valuable bird breeds I have never been able to discover" (p. 74). These 'Ortolans' are in fact young Reed Buntings (see Hildebrandt 2007: 162, footnote).

Heidelerche [Wood Lark] (pp. 74–76): "In the breeding season they stay near trees and sing from them, but when they are migrating they no longer perch in trees. They dislike being in open fields" (p. 75).

Krammetsvögel ['juniper birds'] (p. 77): This name is used in our region for thrushes, Blackbird, Fieldfare, Mistle Thrush and Waxwing "because they all have the same character and all like to eat juniper berries." They are described as follows:

Drosseln [thrushes] (pp. 77–82): The *Zippdrossel [Song Thrush]* is the first to arrive in spring. They migrate mostly at night, as do Robin and other small birds. By day, for their food they search for berries in the hedgerows as well as for insects and worms, etc. in meadows. The *Weindrossel [Redwing]* is slightly smaller than the Song Thrush and is dark red on the flanks and under the wings.

Amsel [Blackbird] (pp. 82–84): There are three kinds: (a) *Ringamsel* or *Schildamsel [= Ring Ouzel]*, (b) gray Blackbird [= female] and (c) black Blackbird [= male]. They migrate at night.

Schnarre or *Schnarrziemer [Mistle Thrush]* (pp. 84–85): This is the biggest of the 'juniper birds' and likes to be in large woodlands with grassy clearings. Their contact call is a rattling sound.

Ziemer or *Krammetsvogel [Fieldfare]* (pp. 85–88): The Fieldfare probably breeds in Poland, Russia, etc. Irregular movements in winter.

Seidenschwanz [Waxwing] (pp. 88–89): Eats rowan berries and is a winter visitor which does not appear every 5 or 7 years but occurs irregularly, whenever it likes, just like all other birds that do not appear regularly or at definite times. It probably comes to us from colder countries since it is one of the largest winter visitors and appears only in the hardest winters. "They come in large flocks and readily come down [to the trapping ground], so that one can expect to catch even the last one" (p. 89).

Schmiel, Dompfaff or *Gimpel [Bullfinch]* (pp. 89–91): A well-known bird. "If one can obtain them young then they will easily learn to whistle all kinds of songs, like the Linnet. Where they nest I cannot say because I have never seen a Bullfinch, let alone a nest, in this area in the breeding season (*footnote*: they breed in Bohemia, Thüringen, Hessen, etc.). They do not come to us every year but usually every second year."

Staar [Starling] (pp.122–124): A well-known bird, which (if trained when young) will learn to whistle and speak. "As soon as they have raised their young they gather in large flocks and fly to damp meadows with wet places where reed grows, where they roost at night. Whoever wants to make a decoy to catch them should not live too far from such areas where the birds gather, because while the birds are not actually migrating they simply go where

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food is to be found, so it can be assumed that they will not move far from their usual haunts. The time to catch them starts at Whitsun and lasts until harvest time. Then the Starlings go to the pastures where cattle graze and forage for food there until autumn, when they move away" (p. 122).

Raubvögel [birds of prey] (pp. 124–126): Some species are dealt with here which are often responsible for killing the bird-trapper's decoy birds. The *Habicht* and *Sperber [Goshawk* and *Sparrowhawk]* (in both of which there is a larger [= female] and a smaller kind [= male]). They pursue small birds and are the worst culprits at the trapping ground. They are "the sparrow's greatest enemy, which they even attack, without the slightest fear, in the farmyard where they feel safe. They do not even hesitate to chase them right up to open stable doors or windows" (p. 125). The *Lerchenfalk [Hobby]* is as big as a small Sparrowhawk and just as pernicious; "even if it mostly takes larks in the fields a few times, it soon gets an inclination to eat woodland birds too, but one has to watch for it especially at a trapping ground set up for Wood Larks" (p. 126). "The remaining birds of prey do no damage at the decoy, except in winter when they become hungry. So it has often happened to me that the *Großer Mausehabicht [Common Buzzard]* has attacked my Fieldfare cages, and at that time of year one cannot trust any bird" (p. 130).

Krückelstern and *Neuntödter* (pp. 126–128): There is the large [*Great Grey Shrike*] and the small Krückelster [*Woodchat Shrike*] and the Neuntödter [*Red-backed Shrike*]. Many of the Great Grey Shrikes stay here in winter. They "feed on birds, beetles, and small frogs, and like to make their nests in wild pear trees which stand isolated in the fields" (p. 126). "The Woodchat Shrike is a good bit smaller with a red cap on its head and also nests in trees." Red-backed Shrikes nest in thorn hedges. This species and the Woodchat Shrike are summer birds, "and before one has begun to catch Chaffinches they are already gone". All of them can be very harmful at the trapping ground because they can attack the decoy birds through the bars of the cages. "It is said that the Red-backed Shrike must kill nine kinds of worm, larvae, etc., and when it is sated sticks the remainder onto thorns; although this sounds ridiculous I have actually found it to be true that it spears worms, etc. on thorns when it has eaten enough, in order to eat them another day. And it can often happen that it does not find them again, or has been chased away from the area; for example I once found a little frog, neatly impaled through the mouth on a pointed dry twig and completely dried out. When these shrikes pull their prey apart they do not hold it under their feet, so they have to stick it on a thorn or pointed twig to be able to pull pieces off according to their appetite" (pp. 127–128).

Heher and *Holzschreyer* (pp. 128–130): There are two species, one of which is called *Nußheher* or *Holzschreyer [Eurasian Jay]*. It is very common in the forests. "The other species is not so common and is seen in our region only very rarely, and I have encountered it only twice in 22 years. They are the same size as the former and look completely black with white spots like the Starling and white bands on the tail. Some call it the *Tannenheher [Nutcracker]* and others the *Nußheher*. Nußheher is a good name for it because it likes to eat nuts, which I have never seen the Jay do. Their migration is at the same time as that of the Song Thrush, and they sometimes appear in large flocks. They eat all kinds of vermin and tree fruits" (p. 129).

Kreutzvogel or *Krinitz [Common Crossbill]* (pp. 130–132): "Around the year 1760 in the month of August 2 of these birds were seen in my copse, sitting in the rowan trees and splitting the berries apart to eat the seeds.

I immediately made a snare and hung it among the berries, and when I returned I had caught the female but the male was gone. This female looked yellow and had black wings and a black tail. I fed her with hemp seed and oats which seemed to do her good; she had a quiet and charming song, this being an unusual thing among other birds. The cock was red on the sides and front of the breast, almost like a Chaffinch. In the spring of 1786, in the breeding season, another pair appeared, the cock of which looked just like the previous one and had a strong and beautiful song that could be heard at a distance.

However the female was ashy gray with brown cheeks, and below her tail were several brown feathers. They built their nest in a loose hedge, about 6 feet [*2 Ellen*] above the ground, of dry stalks, like a warbler's nest, lined with horsehair. The eggs were like those of a Red-backed Shrike in size and appearance, though spotted with light red not dark red like the shrike's eggs. They had 4 eggs.

Apart from these I cannot recall having seen Crossbills in our area. Which is why I cannot include them in the migratory birds; their proper home is supposed to be in spruce forests, where they feed on the seeds from the spruce cones; they hold the cone with their strong and sharp claws while they extract the seeds with their hooked bill, like the Siskin does with alder fruits.

[…] Otherwise I have heard it said that these birds […] do not breed in spring like the others but in January. Although this sounds foolish, anyone who has no experience of the matter should believe it until more definite information is available, and this is why I have described my own experience of these birds at such length, from which the reader can see how tireless my efforts have always been to discover the real nature of bird-trapping" (pp. 130–132).

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II. On other woodland birds, their food, feeding and trapping (pp. 133–161)

Guckguck or *Kuckuk [Cuckoo]* (pp. 133–135): It is not a bird of prey although it looks like the small Sparrowhawk; however, bill and claws are more like those of the Blackbird. "When it sits on a twig it grasps it with two toes behind and two in front, which no other birds do but the woodpeckers. […] Its food mostly consists of caterpillars, beetles, butterflies, and all kinds of worms; hence they often swoop to the ground to take earthworms" (p. 133).

"Because the Cuckoo does not raise its own young, the Creator has made it part of its nature to lay its eggs in the nest of another bird which incubates them and rears the young as its own. It never lays more than one egg [in a nest], and always chooses the nest of a bird that feeds its young with food that agrees with the Cuckoo's nature. It throws the bird's own eggs out of the nest with its bill, and since this often results in most of the eggs being broken, some have thought that it sucks the eggs, but this is false because I have found both whole and broken eggs below nests.

It often lays its egg in the nest of a wagtail or a warbler, which is proof that it cannot be a bird of prey because if it were it would lay its eggs in their nests since they feed their young with all kinds of meat. Some say that when the young Cuckoo has been raised then as a sign of gratitude it eats its foster parents, and even claim to have seen how it snaps at them, but all this has as little basis in fact as what has been formerly said. If it snaps at them then either from hunger or from anger at having been brought too little food, for the wagtails have their work cut out just to satisfy such a large bird. I have watched in my own garden how a pair of wagtails fed a young Cuckoo, and they stayed in the same place long after the Cuckoo had left the nest and could feed itself.

After this I raised young Cuckoos and shot adults, and having dissected them and examined their nature I could find not the slightest evidence that they were raptors. If we just look at the Red-backed Shrike, although it is the smallest bird of prey it still has a hooked bill and powerful claws, both of which the Cuckoo does not have. It ceases to call around St. James's Day [= 25th July] and then forages for its food in silence, and departs before St. Bartholomew's Day [= 24th August]. Because it stops calling just when the fields are being harvested, when the Hobby comes to forage, and since the Hobby at a distance can resemble the Cuckoo, then ignorant people say that the Cuckoo has changed into a bird of prey. The songbirds mob it, and when they see it they pursue it with biting and nipping. The Cuckoo defends itself by biting back, but I have never seen that it would chase one or kill it, although I have sat for many hours in the woods watching for this. Whether this mobbing by the small birds comes from the Cuckoo's looking like a raptor or from its sometimes being caught at the nests one cannot know for certain, though the former seems more likely to me than the latter. The Cuckoo is on the whole a useful bird in the garden because it feeds mostly on caterpillars, and in the spring it is one of the most agreeable of the messengers that announce pleasant summertime to us" (pp. 134–135).

Wiedehopp [Hoopoe] (pp. 136–137): "Its song consists of a hollow note that sounds like hop, hop, hop. It feeds on worms in the earth and other kinds of larvae, etc. It makes its nest in hollow trees and because it smells so horribly in the cavity some people say that it uses human excrement in its nest, but this is wrong since the smell comes from the bird's own droppings. […] It arrives not earlier than April, when it becomes properly warm, and leaves, like all summer visitors, during the month of August."

Spechte [woodpeckers] (pp. 137–139): There are 6 species: *Grünspecht [Green Woodpecker]*, *Schwarzspecht [Black Woodpecker]*, *Großer Buntspecht [Great Spotted Woodpecker]* (in spring this one seeks "a dry broken end of a branch and drums on it with its bill […] instead of a song"), *Kleiner Buntspecht [Lesser Spotted Woodpecker]*, *Blauspecht [Nuthatch]*, and *Grauspecht or Wendehals [Wryneck]*. "The little *Baumläufer [treecreepers]* are also included in the woodpeckers; they are as big as a Siskin and have a long curved bill to dig out tiny verminous animals from the cracks in trees."

Meisen [tits/chickadees] (pp. 139–142): We have 5 species: *Kohlmeise [Great Tit]*, *Blau-* or *Pümpelmeise [Blue Tit]*, *Plattmeise [Marsh Tit]*, *Tannenmeise [Coal Tit]*, and *Spiegelmeise [Long-tailed Tit]*. An exact description of the 'tit-dance' follows, used to catch these species, in which a bird with broken feet flutters around.

Kernbeißer [Hawfinch] (p. 142): The Hawfinch or *Kirschfink* [Cherry Finch] bites a cherry stone as if it had been split by a knife; they also like to eat hemp seeds. They are only caught singly on the trapping ground.

Spanier [Dunnock] (p. 143): Migrates singly and mostly at night; they are only caught as singletons on the decoy. "Where they breed I have not been able to discover."

Nachtigall [Nightingale] (pp. 143–144): This bird is well known, it nests close to the ground. "It mostly returns to the same place to build its nest. It departs during the month of August." They can be caught on the trapping ground for Chaffinches.

Pfingstvogel [Golden Oriole] (pp. 144–145): "It builds its nest in trees, and it always looks for a narrow branch that does not grow straight upwards but has a fork at the end. In this fork it makes its nest, which hangs in the air, not

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supported on a branch like that of other birds. […] It is the largest summer visitor, leaving in August and returning to us only in May. It eats especially cherries and elderberries."

*Weißkehlen [*Sylvia *warblers]* (pp. 145–146): There are 4 species: (1) *Grasemücke* with white throat *[Garden Warbler]*, (2) *Kleine Weißkehle [Lesser Whitethroat]* is brown on the wings, (3) *Fliegenschnäpper [Common Whitethroat]* is smaller still and has an ash-gray head and snow-white throat, and (4) *Plattmönch* or *Murrmeise [Blackcap]*: "The cock has a black cap on his head and the female a brown one. This bird has a beautiful song that almost sounds musical, and when the other birds stop singing around St. John's Day [= 24th June] this one is just getting started and sings until St. James's Day" [= 25th July]. In the autumn it feeds on berries like the Fieldfare, and departs in September and October. The 3 other species migrate in August and September, return to us again in April and nest in hedges.

Schackruthge [Icterine Warbler] (p. 146): "It arrives with the Golden Oriole in the month of May, and departs with it in August. Its song is exquisite and powerful."

Fitis [Willow Warbler] (p. 147): Looks similar to the Icterine Warbler but is smaller and has a pale stripe over the eye, and also stays longer.

Distelfink or *Fliegenschnapper* (pp. 147–148): There are 2 species of *Distel-*, *Lohr-* or *Spießfink*, namely large *[Spotted Flycatcher]* and small *[Pied Flycatcher*, female and brown male]. The small ones look similar to female Chaffinches, but eat mainly insects and live in low thorny and thistly hedges. "They are as big as Lesser Whitethroat, and nest in hollow trees." The large one is light gray and appears slightly scaly. It makes its nest of moss, like a Chaffinch's, on the old branches of trees and on pollarded willows.

Rotschwänze [redstarts] (p. 148): There are 2 species: the common *Rotschwanz [Common Redstart]* nests in hollow trees as well as in crevices and holes in walls. The *Schildnachtigall [Bluethroat]* "searches for its food almost always on the ground and is often found in ornamental gardens as well as those where cabbage, lettuce, beans and such plants are grown. It has a beautiful song and sings at night like a Nightingale. […] In the months of August and September it migrates.

Rothkehlgen [Robin] (p. 149): A well-known bird which departs in September and returns in March. The young are scaly brown, without a red throat.

Zaunkönig and *Goldämmerchen [Wren* and *Gold-/Firecrest]* (pp. 149–150): The Wren has a very strong voice for the size of its body. The Gold-/Firecrest is slightly smaller, has a yellow stripe on its head and always moves around in the company of tits. [Firecrest and Goldcrest were only distinguished in the 19th century.]

Rohrschliefer or *Rohrsperlinge* (pp. 150–151): There are 3 species: (1) the *Große Rohrsperling [Great Reed Warbler]* lives on lakes and marshes with reedbeds, builds its nest over the water and sings day and night, (2) the other species *[Eurasian Reed Warbler]* is as brown as the second *Weißkehle [Lesser Whitethroat]*, also lives in reeds on lakes but its song is not so loud. (3) "The third species is slightly smaller again, looks rather like a Dunnock and has a light-brown stripe mixed with yellow on its head *[Aquatic Warbler?]*. Its song resembles the chirruping of a cricket or grasshopper, which is given in one long breath [?]. They all nest above water in sedge and reeds, or in shrubs among willows. They feed on all sorts of worms, etc. from the water and depart with the summer visitors."

Spießlerche [Tree Pipit] (p. 151): "Breeds in the woods and builds its nest in grass on the ground. It has a rather attractive song, and when it sings it flies high above the trees, letting itself down onto a tree, singing all the while. It migrates in August and September."

Krautlerche [Whinchat] (pp. 152–153): "Its shape is altogether very like that of the Wheatear, only it is smaller. In spring it remains in young tree plantations and field hedges, where it nests; it likes to build its nest in meadows, in the grass. It has a beautiful song; in the middle of August it starts to migrate and then is only found in the fields, especially among cabbages.

Bachstelzen [wagtails] (pp. 153–154): The blue wagtail or *Ackermann [White Wagtail]* is one of the earliest summer visitors to arrive in spring. It nests in hollow trees, thatched roofs and on river banks, etc. The *Gelbe Bachstelze [Yellow Wagtail]* belongs to the field birds and frequents meadows and fields. It arrives later than the White Wagtail in spring and is a welcome messenger for the farmer because it heralds the summer.

Tageschläfer [Nightjar] (pp. 154–159): A nocturnal bird with a thin bill. "But when it opens the bill its whole head splits in half, like a pair of pincers. During the day it sits and sleeps below hedgerows on roots and stumps, as well as in the middle of forest rides, and sleeps, so that it can often be mistaken for a piece of tree bark. At night, on the other hand, it flies around feeding on gnats, beetles, and all kinds of small animals, which it skillfully catches in the air. It is a summer visitor and as soon as it finds no more flies it moves elsewhere."

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Waldschnepfe, *Becasse [Woodcock]* (pp.159–160): The Woodcock has a soft bill, its food is earthworms, slugs and larvae in the soil. "During the day it forages for food under hedgerows, and in the evening when twilight begins it flies to the meadows and arable fields and looks for food there; they make their nest in grass on the ground, but that is something rare in our region. They migrate in October and return in March and April; they migrate in the night; when they start off at twilight they call loudly, making a sound almost like the chirruping of young chickens; they only do this in spring though, not in autumn."

Wilde Tauben [wild pigeons] (pp. 160–161): The biggest species is the *Ringeltaube [Wood Pigeon]*; the common *Holztaube [Stock Dove]* is rather smaller than the domestic pigeon. The *Turteltaube [Turtle Dove]* is smaller, light brown with a black-gray tail. Wild pigeons nest in trees, and depart in autumn to return in spring.

III. On birds of prey (pp. 162–173)

Krähen [crows] (pp. 162–164): There are 6 species: (1) *Rabe [Raven]* with its gruff, staccato voice and wedge-shaped or round tail (straight as if cut off in the crows); not as common as the crows; (2) *Schwarze Krähe [Carrion Crow]*, similar to the Raven but smaller; (3) *Schildkrähe [Hooded Crow]* is just as big as the previous one, black but with ash-gray belly and back. These last two crows have "a single nature and characteristics, so much so that they sometimes mate with each other". (4) The black *Feldkrähe [Rook]*; the bill is weaker than in the previous species, and the skin towards the head rough and white. They damage root crops but this harm "is not by a long way as great as the good they do because they eat all the creatures harmful to crops like caterpillars, beetles, grasshoppers, etc." (p. 163). (5) *Dohle* or *Schneekrähe [Jackdaw]*, black with an ash-gray neck. (6) *Blaue-* or *Mandelkrähe [European Roller]*. They feed on beetles and other vermin, do not take smaller birds, and do not associate with the other crows. "They belong to the summer visitors, but are not seen so frequently as the others."

Elster [Magpie] (pp. 164–1165): A well-known and very injurious raptor that searches for nests of Pheasant and Partridge and hunts young Pheasants, Partridges, ducks and hares. When they realize that someone is climbing their nesting tree "they carry their young away to another nest, and so it is probable that they have two nests".

Eulen [owls] (pp. 165–166): There are 5 species: (1) The *Uhu* or *Schuhu [Eagle Owl]* "is the largest, it lives in the high hills and is seldom encountered in our area". (2) The *Knappeule [Tawny Owl],* brown mixed with ash-gray, "a harmful visitor to dovecotes, which it frequently enters at night to pull out the young pigeons". (3) *Horn-* or *Ohreule [Long-eared Owl]*, smaller than the previous one, dark gray with two feather 'ears'; (4) *Kohleule [Short-eared Owl]*, brown like a Tawny Owl; "it is often found in fields, among cabbages, also in meadows and in long grass". (5) *Kauz [Little Owl]*, the smallest species and pale gray, nests in hollow trees, old walls, and buildings. "Since owls are not seen during the day birds are not used to them, and their mobbing behavior is sometimes shown even towards the Nightjar, although it is not a bird of prey" (p. 166).

Falken ['falcons'] (p. 166): "The *Adler [White-tailed Eagle]* is the largest of them, but is seldom seen in our region. It is black-gray in color with white spots [?]. The bill is one inch straight and then is hooked at the end, which distinguishes it from other birds of prey. The *Steinadler [Golden Eagle]* is slightly smaller".

Mausehabichte [Rough-legged and *Common Buzzards, with color morphs]* (pp. 166–168): There are 5 kinds: (1) Plumage dark black-gray, speckled a little with white on the breast and under the wings. (2) Similar to the first though not colored blackish but brownish, and with more white speckling on the breast and under the wings; this is the commonest kind; (3) similar to the previous two, "except that this kind has shaggy feet like an owl" [Rough-legged Buzzard]; (4) also similar, but with a longer tail and white rump; (5) with a longer tail and longer wings, speckled with gray, brown and white.

Fischaar [Osprey] (p. 168): Hunts mainly fish, "then they hover in the same spot in the air until they see a fish, when they shoot down and under the water like a duck, seize the fish, and fly off with it. It does not remain here in the winter". Its legs are covered with rough skin, like a woodfile.

Weyhen [harriers] (pp. 169–170): There are 4 species: (1) *Gabelgeyer [Gabelweihe = Red Kite]*; it flies slowly and cannot catch any prey in the air; hunts young ducks and geese; (2) *Moosweyhe [Marsh Harrier]* only found near water and marshes; (3) *Kleine Weyhe [Montagu's Harrier*], also known as the *Milane [kite]*, smaller than the previous one, pale gray with a white rump, yellow legs, and white belly and breast streaked with black, "flies slowly and low, always looking down at the ground"; (4) *Weiße Weyhe* or *Weißer Falke [Hen Harrier]* is not as big as the previous one, white shading to ash-gray, wing-tips black, legs yellow. Shape and behavior as the previous harrier. All harriers leave in the winter.

"The small *Rudelgeyer [Common Kestrel]* can also be included in the harriers. […] It can hover for a long time in the same spot in the air by continuously steering or fluttering with its wings, hence its name of Rudelgeyer ['rowing raptor']. It lives mostly on mice/voles" (p. 170).

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Blaufuß [Peregrine Falcon] (pp. 171–172): "In our region we have two species of falcon. The large one is called Blaufuß ['blue foot'] and the other is the small *Lerchenfalke [Hobby]*. The Peregrine Falcon is "the worst enemy of Partridges and pigeons. As soon as it spies a flock of pigeons it looks for the slowest one, mostly selecting the white or colored ones. It shoots towards them like an arrow, but if the pigeon succeeds in reaching a hedge, tree, or water (since a pigeon can dive in water like a duck, which I have seen with my own eyes) then the falcon will retire. But if the pigeon does not manage to reach such safety it will fly as fast as possible, skillfully avoiding the falcon's attempts to seize it by flying higher, though the raptor will try to climb above it, then the pigeon repeats the procedure. If the pigeon succeeds again and again in being higher than the falcon then the latter will finally tire and turn away, allowing the pigeon to escape, which I have often observed. Otherwise it is a shy bird and difficult to shoot."

IV. On field birds (pp. 174–184)

Trappe [Great Bustard] (pp. 174–175): The largest field bird, nests on the ground in cereal fields, lays 2 eggs, eats green crops and plants, does not migrate in autumn and can only be caught with some cunning.

Krannich [Common Crane] (p. 175): A very cautious passage bird.

Rebhühner [partridges] (p. 176): There are (a) *Reb-* or *Buschhühner* and (b) *Feldhühner*, which breed respectively in copses or in fields. But it is not said whether they differ in their plumages.

Wachtel [Common Quail] (p.177): Returns in May and leaves again in autumn. They do not live in groups like the Partridge "but mostly fly around alone".

Wachtelkönig, Schnarker [Corn Crake] (pp. 177–178): The Corn Crake "breeds in meadows and cereal crops and migrates with the Quails; it does not lay many eggs which is why they are not as numerous as Quail. […] Their song sounds like the creaking of a door and is not exactly pleasant to hear".

Lerche [Sky Lark] (pp. 178–179): "It is widely known what kind of bird the Sky Lark is, it arrives here in March and nests in our fields. […] Because the Sky Lark has a beautiful song it is kept by many people in a cage and fed with oats".

Hüster [Meadow Pipit] (p. 179): "The Meadow Pipit is in shape and color very like the Tree Pipit, though a little smaller and less yellow, but otherwise it is of exactly the same character. It is a bird of the fields and is caught along with the Sky Lark; they prefer to be in green crops."

Schneelerche [Snow Bunting] (pp. 179–180): "A rare bird and little known. It is only seen in winter, especially when there is much snow on the ground, at the end of December and in January; they are only found singly and eat all kinds of small seed-heads sticking through the snow; they are smaller than Sky Larks, white in color with gray breast and back, and have a peculiar call; it is supposed that these birds breed in very cold countries, and only at certain times, when the coldness there is very great and food scarce, do they migrate to our region: they do not appear every year; it is the same with the Waxwing, and we have no other winter birds but these two species."

Steinpicker or *Steinklitsch [Northern Wheatear]* (p. 181): "It occurs in fields in the high hills, it builds its nest on river banks or in rock crevices, also even in mole holes. […] According to its character it has much in common with the Whinchat."

Kiebitz [Northern Lapwing] (pp. 181–182): "Its habitat is wet meadows and arable fields, it makes its nest on [*Kufen*?] and in clumps of rush. […] In the autumn they gather in large flocks and get ready for migration."

Brachvögel [Curlew, etc.] (P. 182–184): Four (or five) species – (1) *Keulhaken [Eurasian Curlew],* (2) *Saatvogel [European Golden Plover]*, (3) *Dütgen [Dotterel]* and *Kleiner Brachvogel [Whimbrel]*. "I once saw another kind of *Brachvogel*, which was no bigger than a lark and looked almost like a White Wagtail."

V. On waterbirds (pp. 185–199)

Schwan [Mute Swan] (p. 185): "It can be easily tamed and is kept as an ornamental bird by the gentry." It migrates in small groups in spring and autumn, and feeds on plants.

Wilde Gänse [wild geese] (pp. 185–187): The wild goose is ash-gray with a white belly; it breeds in marshy places and is a migratory bird, but some also stay here in winter, when they feed on "green cereal crops and grass". "Their migration is wonderful to see; no other bird pays more attention to discipline and caution than Cranes and geese; they always fly in the form of a triangle, at whose peak is always an old gander that is akin to the leader of the whole army. Whoever wants to shoot them must use all his cunning.

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Wilde Enten [wild ducks] (pp. 187–189): (1) Common wild duck *[Mallard]*; nests on old pollarded willows or at the water's edge; departs in autumn, though many stay here; breeds with farmyard ducks; (2) Smaller, with a short blue bill, head of male brown with whitish gray on the wings *[Common Pochard]*, (3) *Große Krückenente [Garganey]*, (4) *Kleine Krückenente [Eurasian Teal]*, (5) *Große Löffelente*, tail long and pointed like that of a pheasant *[Pintail?]*; (6) Bill like that of Pintail [?] but tail short *[Shoveler]*. (7) *Große Tauchente*, larger than Mallard, ash-gray, head brown, bill and legs red, very rare *[female Goosander, Red-breasted Merganser]*, (8) *Kleine Tauchente* or *Pfeifente [Eurasian Wigeon]*, "because it can whistle just like a person does with his fingers. […] They often dive below the surface and are skilled fish-catchers [?]." (9) *Weiße Tauchente*, head and wing-tips black, very rare *[Goldeneye]*. These diving ducks migrate in autumn and return in spring.

Reiger [Grey Heron] (pp. 189–190): "It does not carry its neck stretched out when flying, like the stork, but doubles it over. […] Its food is fish, frogs, and shellfish."

Rohrdommel [Eurasian Bittern and *Little Bittern]* (pp. 190–191): Large and small bittern. "When the Bittern is sitting and notices somebody approaching then it stretches its bill, neck, and whole body straight upwards, without making any other movement, so that it looks like a pointed wooden post or old tree trunk. […] When it wants to call then it puts its bill under the water, which increases the volume so that it can be heard at a great distance." On p. 155 Naumann wrote that he had observed how the Bittern puts its bill "under the water" when calling. "I spent a lot of time stalking them before I was able to see this, until once I was successful and, luckily, in bright moonlight saw it because the bird went down to the water." — In size and character the Little Bittern is similar to the larger species, and "when it sits in a tree it points its bill and body straight upwards and so could be mistaken for a pointed branch".

Möwen or *Seekrähen [gulls* and *terns]* (p. 192): There are three species: (1) The large Seekrähe *['sea crow' = Common Tern]*, as large as a pigeon, it is white and has a black cap on its head, and a hooked and sharp bill; (2) Thrush-sized with longer wings, ash-gray, and in behavior similar to the first species *[Black Tern]*; (3) All white and not so common as the previous two *[Black-headed Gull, non-breeding plumage]*.

Eisvogel [Common Kingfisher] (pp. 192–193): The 'water-woodpecker' "always sits on the branches of trees that hang over water and when it sees some worms in the water it dives down into it, seizes a worm, and flies back up to its perch on a twig or post."

Hurbel or *Blösse [Coot]* (p. 193): The Coot is constantly on the water and lives on small fish and all kinds of water worms, etc.; they build their nests in the reeds on the water, and move away in the autumn.

Wasserhüner [waterfowl] (pp. 193–194): 3 species with long narrow toes: (1) The *Große Wasserhenne [Moorhen]* with red shield above the bill, (2) very like that species but no larger than a Quail *[Little Crake/Water Rail?]*. (3) Black speckled with white, and with many white feathers in the tail *[Spotted Crake]*.

Taucher [grebes] (pp. 194–195): (1) *Großer Taucher [Great Crested Grebe]* is "more seldom seen than the small one; they have a pointed bill; […] they dive constantly and live on fish". (2) *Kleiner Taucher [Little Grebe]* "is as big as the small *Wasserhenne* and they are the commonest [grebe]".

Wasserschnepfen [waders] (pp. 195–199): "The names are very uncertain for in one place they are given one name, in another place a different one. Everyone should call them by the name that is used in their area." [For curlews and plovers see above under Field Birds.]
Große Wasserschnepfe [Black-tailed Godwit], call 'kla – rit'
Große Pfuhlschnepfe, legs olive-green *[Greenshank]*
Kleine Pfuhlschnepfe, coloring similar to the previous one *[Wood Sandpiper]*
Similar to Dotterel but with a longer, finer bill *[Common Sandpiper]*
Großer Rotschenkel [Spotted Redshank], ash-gray and speckled white, white rump, red legs, call 'ta – it'
Kleiner Rotschenkel [Common Redshank], like the previous one but smaller.
Followed by various species of stints and sandpipers that cannot be identified on the basis of the descriptions.

Bekassinen [snipe]: (1) *Ketschnepfe, Gras-* or *Riedschnepfe [Common Snipe],* (2) slightly smaller *[Jack Snipe]*, does not fly so rapidly

VI. On tame birds

"Tame birds are what I call those that live in towns and villages, and which prefer to be around people."

Storch [White Stork] (p. 200): "It likes to build its nest on buildings, especially on thatched roofs, as well as in high trees. There is also another species of stork *[Black Stork]*, which is coal-black with a white belly and breast, but it is found much less frequently."

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Schwalben [hirundines] (pp. 200–201): The *Haus-* or *Stachelschwalbe [Barn Swallow]* nests in buildings and stables. The *Mehlschwalbe [House Martin]* "hangs its nest on the outside of buildings, closing it up except for a small hole through which to enter".

Haus- or *Sallatlerche [Crested Lark]* (p. 201): Slightly larger than the Sky Lark, with a pointed crest on its head; it has a very pleasant song, builds its nest in gardens underneath the garden plants or on walls, most likely also in thatched roofs. "It is not found everywhere, only in upland villages with few trees around the buildings and adjacent to open fields."

Sperlinge [sparrows] (pp. 201–202): *Haussperling [House Sparrow]* and *Holz-* or *Rohrsperling [Tree Sparrow]*, "the latter is slightly smaller and has a brown head. At the end of this book I will put both of these sparrow species on the stage, where they will tell each other about how they live."

Two years after the appearance of *Der Vogelsteller*, J. A. Naumann published a further small book:

Der philosophische Bauer
oder Anleitung, die Natur durch Beobachtung und Versuche zu erforschen (1791)

[***The philosophical farmer***
or instruction in the investigation of nature by observation and experiments].

A new edition in a different format was published by Paul Leverkühn (1900), with an introduction and detailed annotations by the editor.

Naumann speaks here on nature, weather forecasting, anthropology (temperament and physiognomy), alchemy, honeydew, ergot, mildew, on the immutability of matter and its quantity, on chemical processes, as well as on bird migration and birds as weather "prophets" (Siskin, Redpoll, Fieldfare, Waxwing, Snow Bunting); to the latter observations Leverkühn (1900) commented in detail, drawing on later research.

This little book (19 x 11.5 cm) contains, as Baege (1980: 6) wrote, "all kinds of reflections on occurrences in nature, but so peculiar were some of his explanations that one scientist felt obliged to advise the farmer to stick to his plow" (see Leverkühn 1900: 63–64 and Allgemeine Deutsche Bibliothek, Volume 110, Kiel 1792, p. 451).

Johann Matthäus Bechstein (1757–1822*).* Bechstein (Fig. 21) was initially a schoolteacher at the Philanthropin in Schnepfenthal and later, while he was Director of the *Forstakademie* [Academy of Forestry] in Dreißigacker near Meiningen, the first biologist among the founders of scientific forestry (Hildebrandt 1933; Mey 2003): "He was the first man to give forestry studies a sound scientific foundation, sending emissaries to spread his ideas rapidly through the whole of Germany" (Ratzeburg 1872)[4]. Bechstein recognized the necessity of regarding the whole of nature as a unified interdependent organism and saw that: "Nature is in balance when left to herself!" (*Musterung der Thiere……* 1792a, Introduction p. 4) [*Review of the animals*…….]. An initial propagation of the idea of bird protection was introduced in his work. Bechstein left an enormous life's work in several fields at his death, but "in all of natural history my favorite subject has always been ornithology" (1791, Foreword, p. V). He was an experienced field ornithologist, who roamed through the *Thüringer Wald* and its surroundings on numerous excursions, and who constantly kept 30–60 birds of different species in large aviaries at his home, observing their movements and behavior. "I dare say that there is probably no bird in Germany, at least not in Thüringen, that I would not be able to quickly identify at a good distance by its voice and flight" (Foreword, pp. VIII–IX, footnote). Johann A.E. Goeze (1731–1793), a physico-theologian in Quedlinburg who knew Bechstein well, wrote to him on March 16th, 1792: "If only I could go hunting with you! We wouldn't want to shoot, just observe" (L. Bechstein 19855: 32).

Just like the natural history research of his forerunners, Bechstein's work was also done in the light of physico-theology. In the Foreword to Bechstein's early work on the *Gemeinnützige Naturgeschichte Deutschlands* (Volume 1, 1789, pp. II–III) [*Popular natural history of Germany*], C.G. Salzmann, Principal of the Philanthropin in Schnepfenthal and a great influence on Bechstein, wrote:

"Nature is […] the book of God, which tells of the power, wisdom, and goodness of its author. […] When I watch them [= the 'useless' insects] when they are on the melons and cucumbers, and I see how they powder themselves with the pollen of the male flowers, how they fly with it to the female flowers, and so in their fashion fertilize them[5], then I cannot help but to look up to the Almighty with a feeling of gratitude that something unknown has been made clear to me.

The more insights I gain in the context of the things I see around me, then the more I come to know the Heavenly Father and the deeper becomes my reverence, my love, my trust in Him."

Bechstein himself asserts in the Foreword to his *Kurzgefaßte Gemeinnützige Naturgeschichte* (1792b: V–VI) [*Shortened popular natural history*]:

"Nothing lets us better know the mighty, wise, and good Creator [than natural history]. The works of God are – and the wise Creator wished it so from the beginning – the schoolmasters of mankind and we their pupils."

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Fig. 21. Portrait of Johann Matthäus Bechstein after a pastel drawing of 1803 by J.P. Bach (from *Rudolstädter naturhistorische Schriften* 11 [2003]. Original in possession of the Meininger Museen der Kulturstiftung Meiningen).

J.A. Naumann's *Vogelsteller* (1789) had appeared two years before Bechstein published the first volume of his avian handbook in 1791, and the latter used passages from Naumann's book in several places: "Entire passages and sentences from Naumann appear in condensed form in Bechstein, as well as a re-engraved copy of a plate, and all unacknowledged" (Baege 1980: 14).

Principal ornithological work. Bechstein's *Gemeinnützige Naturgeschichte Deutschlands nach allen drey Reichen* [*Popular natural history of Germany covering all three kingdoms*] appeared in four large volumes, numbers 2–4 of which dealt with birds (1791–1795) (Fig. 22; online Appendix 3); a second expanded edition was published in 1805–1809. Volume 1 is on the mammals. All birds known to the author in the country are described in great detail, and every species section is consistently divided into field characters, description, characteristics, distribution and occurrence, food, breeding, predators, diseases, usefulness, harmfulness, names, and varieties. When Bechstein began writing his manuscript in 1786, ornithology in Central Europe was still in its infancy. No distinction was made between Ringed and Little Ringed Plovers, Green and Grey-headed Woodpeckers, Great Spotted and Middle Spotted Woodpeckers, or between Goldcrest and Firecrest. Nevertheless, at the end of the 18th century Bechstein's *Naturgeschichte* was the most important and most complete handbook of birds, which were presented in the modern Linnaean methodology, each bird with a Latin genus and species name. In Germany this methodology had been employed in ornithological works since the 1760s by P.S. Pallas and J.R. Forster, and introduced later in larger works dealing with the entire animal kingdom by Statius Müller (from 1773) and Gmelin (1788–1789).

Bechstein defined bird species in a purely morphological-typological fashion: "If several such things [= individuals] have a great resemblance to each other in their important characteristics and parts then they can be considered as the same species. If several species agree in certain principal characteristics then they constitute a genus" (1792b, pp. 7–8). The species criterion of successful sexual reproduction employed since the days of John Ray and Georges-Louis de Buffon and later by German zoologists like Frisch, Blumenbach, Pallas, or Zimmermann, was probably unknown to Bechstein, at any rate he neither used nor discussed it. This meant that in many cases he described individuals of one species but different plumages under several new species names. For example, without any further disccussion he classed the gray- and black-backed Pied Flycatchers, which represent plumage morphs within a variable population, as two separate species. Similarly, he gave newly-devised Latin names to birds in winter, breeding, and juvenile plumages of several species of waders, on a pure morphological-typological basis without any comparative discussion.

In the Foreword to his *Naturgeschichte, Vögel* [*Natural history, birds*], Volume 1 (pp. VIII–IX), Bechstein (1791) wrote:

Fig. 22. Title page and frontispiece of Bechstein (1791–1795; vol. 3, 1793).

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"In order to give my natural history of birds a certain truth to the best of my ability, and to make my way as securely as possible, I have consistently and carefully studied, in all seasons of the year, those birds that I have always had around me (and I think I may count all the species in Thüringen among them), have taught myself their natural history by observing them, and have described the characters of every bird from life, taking exact account of season, sex and age."

As an anonymous critical reviewer of the first bird volume of 1791 (perhaps Blasius Merrem?) remarked, the above guideline was only partly correct, since the author had naturally used many accounts of birds he had not personally seen from other books, "by which his own, often excellent remarks are frequently stifled". The same reviewer continued: "Everywhere apparent is a lack of critical awareness and theory of natural history. […] The author comes to grief completely in the Introduction [on avian anatomy]; it is full of errors." Because of the author's verbosity and digressions "some of his own, often important observations, and the many good aspects of this book, are overshadowed and wasted" (*Allg. Literatur-Zeitung*, October 1792, Vol. IV, no. 265, cols. 53–56).

However, following the completion of the *Naturgeschichte* the work was given a more favorable reception, again anonymous, in the form of a review of the third volume (1795). The reviewer "feels genuine gratitude for the immense efforts made by this ever attentive observer. […] The history of the birds of Germany is brought to an end with this volume. In our judgement it is the most important and richest ornithological work of our time" (*Allg. Literatur-Zeitung*, July 1796, Vol. 3, no. 218, cols. 121–124).

Another anonymous reviewer of the first bird volume praised "this most excellent and, when it is complete, certainly unique work of its kind". The "wealth of the author's own fruitful remarks and observations often throw light on aspects of ornithology all at once that until now had lain in darkness". He goes on to point out gaps in Bechstein's work that he has noticed, (e.g.) there being no mention of Barrington's observations on birdsong, as well as the fact that seabird feathers are water repellent, and "on the whole we would wish to see laying and incubation times given more carefully and more exactly" (*Gothaische gelehrte Zeitungen*, no. 5, pp. 41–48, 18 January 1792).

Bechstein made extensive use of earlier ornithological literature, but recognized that "apart from Buffon's history of birds, most excellently adapted by Professor Otto [in 35 volumes], we in Germany possess no book that deals with this branch of natural history in a comprehensive manner" (1791, Foreword, p. X). The illustration of the Bald Ibis, and the text, are most likely from Buffon's work, as Bechstein was certainly not acquainted with this species. He praised J.L. Frisch as being "in the best possible sense my forerunner in the description of German birds" (1791, Foreword, p. IX), and dealt most thoroughly with his birds using Linnaean methods in his *Natural History*. In the second edition of the *Natural History* he placed this reworking ahead of his own species accounts so that "the lover of ornithology can experience, before reading my description of German birds, the content and manner of Frisch's knowledge" and "because of the excellence of Frisch's work I will always pay close attention to his representations in my accounts and cite them often. As a result, it will also become clear where they should be placed according to the system I use" (Bechstein 1805: 283, 284). Similarly, Bechstein was a great admirer of Freiherr von Pernau's *Angenehme Landlust* (1720), which he himself published in a new 10th edition[6], and he also wanted to edit Pastor Zorn's *Petino-Theologie* (1742–43) but this plan was never realized.

Illustrations. A great weakness of Bechstein's *Popular natural history of the birds of Germany* are the illustrations. Around 100 small depictions show frequently stiff and badly mounted birds, and they are equally unsatisfactory in their coloration. His *Ornithologisches Taschenbuch von und für Deutschland* (1802–1821) [*Ornithological pocketbook of and for Germany*] contains only 39 illustrations and these "are miserable and not worth looking at, apart from the fact that some are simply wrong" (B. Meyer *in litt*. to R.H. Schinz; see Möller 2002). The lack of good illustrations in Bechstein's works was definitely regarded as very annoying by his readers. In an attempt to remedy this deficiency, Bechstein published a general book of plates, not limited to birds, called *Getreue Abbildungen naturhistorischer Gegenstände in Hinsicht auf Bechsteins kurzgefasste gemeinnützige Naturgeschichte des In- und Auslandes* (1793–1809) [*Faithful illustrations of natural history objects relating to Bechstein's shortened popular natural history of Germany and abroad*]. But here too:

"the birds are very more badly drawn from badly mounted specimens. Here the fault does not lie with the engraver or the coloration […] but solely with the drawings prepared under the supervision of the author. […] The illustrations supplied here are hardly in a position to deliver what they are meant to, namely to compensate for the necessary deficiences of a description" (*Allg. Literatur-Zeitung* 1796, Vol. I, no. 46, col. 361–363). (Figs. 23a, b).

Species knowledge. Bechstein knew all the breeding birds of Thüringen, and in his *Naturgeschichte* attempted to deal also with those species which other authors had communicated from different regions, and thus to achieve complete coverage of Germany. However he encountered difficulties with the wading birds, describing the juvenile,

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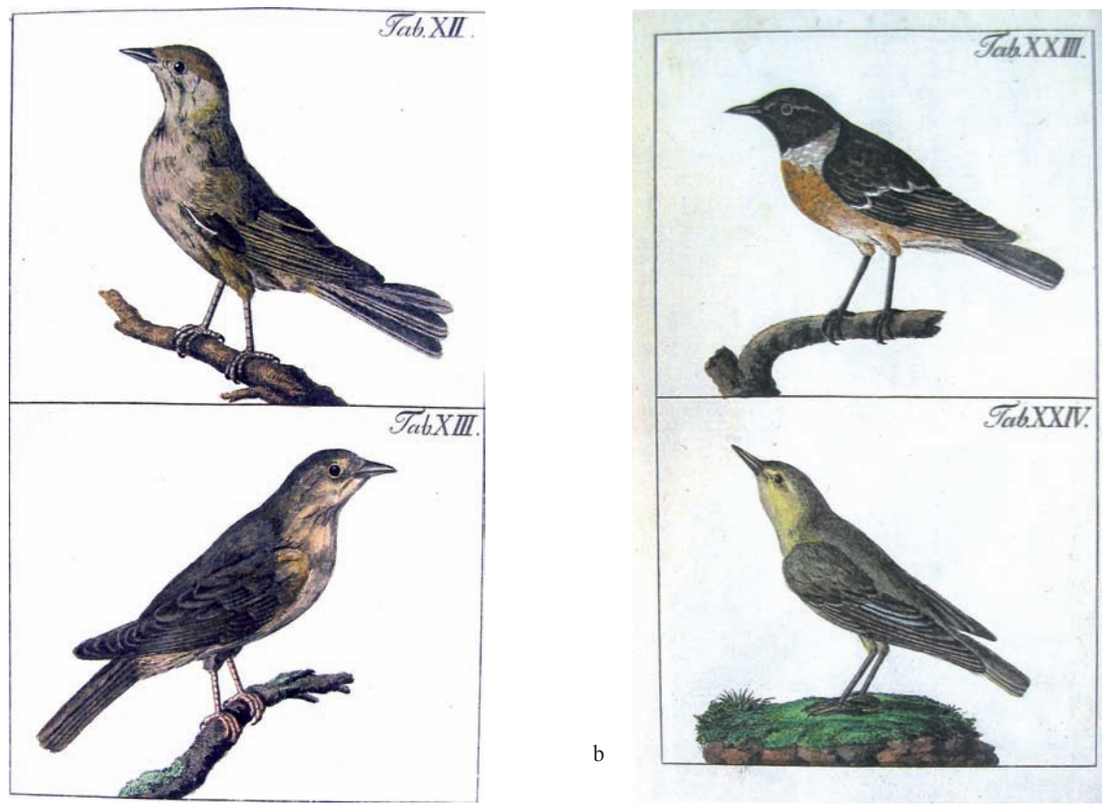
breeding, and winter plumages of several species under different species names.

New descriptions. Bechstein was a field ornithologist and not a systematist, but he did occupy himself with problems of systematics, allocating and publishing many Linnaean species names (consisting of a genus name plus specific name) for birds which, as it seemed to him, had not yet been given names using this methodology. To be able to form an opinion and judge the value of Bechstein's activity in the field of taxonomy it is no longer sufficient to simply "cherry-pick" those names that later had their validity confirmed (Tittel 2002; Mey 2003). Instead, in historical works all names given by Bechstein should be included. After all, in this sense Bechstein himself had allocated and accepted names that are currently both valid and invalid; he held them all to be equally "valid". Moreover, we ought to differentiate between (a) names which Bechstein gave to birds he knew from life or as skins he was able to examine and compare, and (b) those names he attached to a taxon already described in the literature but named only in English, in other words birds that he knew neither from life nor as skins. Bechstein described a total of around 170 bird "species" as new. His assumption, or "hope", that the validity of these names would be assured, was to be disappointed, for only very few of his designations were valid and became established.

(1) *European species and subspecies* (see Mey 2003 and Haffer 2006, *Anhang* [Appendix] 4): Of the almost 100 new "species" names of European birds given by Bechstein only 5(!) refer to genuinely new and at the time unknown species that he had discovered in Thüringen: Marsh Warbler, Collared Flycatcher[7], Red-breasted Flycatcher, Wood Warbler, and Barred Warbler. The Rock Partridge, Barnacle Goose, and Thrush Nightingale that he also named had been known to J.L. Frisch in the pre-Linnaean period, who depicted them in very good color plates. The Marsh Sandpiper had been described by Naumann father and son in 1799 under the non-Linnaean name *Scolopax Glottis minor*[8], also excellently illustrated in color. Hence this species too was not really "new" when Bechstein gave it a Linnaean name in 1803, depicting it in a poor color plate following his collection of the bird as it passed through on migration. The Naumanns had also already described the North American Upland Sandpiper in 1811 under the name *Tringa macroura* (which did not become valid), therefore one year before Bechstein's naming of it as *Tringa longicauda*, based on Latham's published English description. Bechstein described the White-backed Woodpecker in 1802 from a color illustration sent to him



a b

Figs 23a, b. Two plates from Bechstein (1791–1795; vol. 4, 1795, from photocopies by J. Haffer). 23a: female Blackcap (top), Garden Warbler; 23b: Eurasian Stonechat (top), Icterine Warbler.

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from Silesia. The "discovery" of the Parrot Crossbill was occasionally attributed to J.M. Bechstein in his *Ornithologisches Taschenbuch* (vol. 1, p. 106, 1802), as Hartert (1904: 122) noted. Yet here too, B.C. Otto (1778) had clearly differentiated this species from Common Crossbill as "Tannenpapagei" [Fir Parrot], but he did not give the species its own Linnaean name, which was done by Borkhausen in 1793: *Loxia Pytyopsittacus*.

While almost all the scientific names given by Bechstein were applied to species that were unknown to him at the time of their description, most of these birds had in fact already been allocated Linnaean names by other authors. Bechstein's names for them were "redundant" synonyms, an unnecessary burden on nomenclature. A similar unfortunate balance between valid and invalid names exists in the work of other naturalists of the time, who all gave scientific (Linnaean) names (with the additional *mihi* = "by me") to birds and other animals that appeared new to them, in the assumption or hope that the name would later be validated, securing "immortality" for the author's name. But we must pardon these early authorities by reminding ourselves that (a) due to the difficulty of communication and the small print runs of many books they were often poorly informed of current research, and (b) their inadequate knowledge of various plumages and molt stages in some species meant that new names were often given to differently plumaged males, females, or juveniles of the same species. Despite this, the impression remains that Bechstein, as well as some subsequent authors in the 19th century, distributed "new" scientific bird names with a certain recklessness (or *mihi* addiction!). Considering his great experience, Bechstein was clearly aware of the striking molt in some species and therefore understood the necessity of careful comparisons before it was reasonable to allocate a new name. Possibly one of the reasons why he chose to translate the works of Latham and Levaillant in particular (see below) was that they were among the authors who rejected the Linnaean nomenclature, thus affording their translator the opportunity of giving scientific names to the species newly described in their books, in which only common names were printed. It can be assumed, though it is not apparent, that Bechstein knew the differences between the songbirds genuinely discovered by him, and properly described with song, etc., and the many "species" to which he assigned his (invalid) Linnaean names after examining one or two skins, or on the basis of descriptions by other researchers, without any further knowledge of their status.

Bechstein's genus names for European birds that are still valid are *Cygnus* (1803), *Crex* (1803), *Anthus* (1805), *Calcarius* (1802), and *Saxicola* (1802). Several of his remaining genus names were rejected by later authorities (Haffer 2006: Appendix 4). The situation with novel genus names was unlike that of new species names in that he was not dealing with previously unknown birds (unless a new species was placed at the same time in a new monotypic genus), but simply with a new grouping of already familiar species. But also here, with regard to the pipit genus *Anthus*, it should be noted that father and son Naumann (1798) had already separated the larks and pipits as groups, though without giving the latter their own Linnaean genus name.

(2) *Non-European species and subspecies*: In the years 1793–1812 Bechstein translated the great work of the British ornithologist John Latham, *A General Synopsis of Birds* (1781–1785), into German, adding many comments of his own. Latham was one of the ornithologists who thought that the new nomenclature was superfluous and consequently refused to give Linnaean names to any known species or any species newly described by themselves, using English names only. Their discoveries were later appropriated by other authors, who, by supplying these new species with their own scientific names, were "adorning themselves with borrowed plumes". One of these was Bechstein, who, during his translation activities, allotted scientific names to ca. 80 bird "species" that were described for the first time in English or French in works by Latham, Levaillant, and Vieillot. The majority of Bechstein's names were also (invalid) synonyms, but some have survived as valid species or subspecies names (see Peters's *Check-list of the Birds of the World*; the valid taxon is printed in bold in the following list):

Coragyps ***atratus*** (Bechstein, 1793)
Bartramia ***longicauda*** (Bechstein, 1812)
Numenius ***americanus*** (Bechstein, 1812)
Eos squamata ***riciniata*** (Bechstein, 1811)
Trichoglossus haematodus ***capistratus*** (Bechstein, 1811)
Psittacula krameri ***manillensis*** (Bechstein, 1811)
Ara ***ambiguus*** (Bechstein, 1811)
Ara ***tricolor*** (Bechstein, 1811)
Geoffroyus ***geoffroyi*** (Bechstein, 1811)
Upupa epops ***africana*** (Bechstein, 1811)
Dicrurus ***adsimilis*** (Bechstein, 1794)
Phylidonyris ***niger*** (Bechstein, 1811)
Sialia ***currucoides*** (Bechstein, 1798)
Spizella ***passerina*** (Bechstein, 1798)

Among the birds on this list, Bechstein described the parrot *Psittacula krameri manillensis* from a cage bird, perhaps one he had seen in the collection of rare birds belonging to Herzog [Duke] Georg von Meiningen. He knew the others only from descriptions mainly by Latham, attaching his own new Linnaean names to them. Ornithologically speaking, these names are then something completely different from those he gave to the five bird species which he himself had discovered in Thüringen (see above).

Birds have been named in honor of Bechstein only twice, but these names are no longer valid: (1) *Turdus bechsteinii* J.F. Naumann, 1822 [= *T. ruficollis* Pallas,

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1776] and (2) *Tringa stagnatilis bechsteini* Zarudny & Smirnov, 1923 [= *T. stagnatilis*, monotypic].

Reviews of the publications. Although Bechstein was one of the most important Central European ornithologists of the early period, and despite the fact that much has been written on his life and his work as a pioneer of scientific forestry, a thorough analysis of his contribution to ornithology has yet to be undertaken, nor will it be attempted by us here. Mauersberger (1990) has made some comments in this regard indicating the type of approach that should be adopted in this case (and in those of other early ornithologists): (1) determination of the degree to which Bechstein recorded the number of species in Central Europe and clarified their taxonomy; (2) his sources in the literature; (3) the influence of his work on future authors; (4) a comparison of his knowledge of breeding biology and ecology with that of earlier, contemporary, and later researchers, and (5) his field ornithological methods, especially with respect to his *Ornithologisches Taschenbuch*. Only after the application of such a comparative analysis will it be possible to recognize which aspects of ornithological progress in Central Europe follow from Bechstein's work.

In his *Naturgeschichte*, Bechstein generally gave descriptions of a large number of known, but also of then unknown facts relating to European birds, but usually without subjecting them to any kind of biological interpretation, as before him Pernau, and Zorn in particular, had so diligently done. In the general chapter on birds in his *Naturgeschichte* there are the beginnings of such an approach in his function-related terminology of types of foot structure, and in the pointers to the relations between wing length and breast muscle weight or intestine length and diet, as well as species-specific nest materials and construction (Mauersberger 1980, 1990), but the relations between structure, movement, and food choice are not yet grasped. See also Mey (2010) for a good overview.

On his ornithological excursions in Thüringen Bechstein discovered five European bird species (see above). This illustrates just how sharp his fieldcraft and critical attitude were. He had a wealth of knowledge on German birds, which he brought together to great effect in his 3-volume *Naturgeschichte*, to the advantage of the progress of ornithology. However, of the total of 170 Linnaean species names which he introduced into the literature, very few attained permanent validity. As early as 1805, the experienced Herr von Minckwitz wrote to J.F. Naumann: "In my opinion, many birds in Bechstein's *Taschenbuch* are presented as true species which are nothing of the kind" (Thomsen & Stresemann 1957: 56), which was confirmed in the reply from J.A. Naumann: "After my experience with Bechstein's *Orn. Taschenbuch* I would just delete a good few of the species" (see Thomsen 1930: 13). Of the names which Bechstein gave the species discovered by Latham, and allocated only English names by that author, some remain valid. But these are purely "administrative" names, given within the framework of the Linnaean method to species discovered by another ornithologist, and therefore to be regarded in a completely different light from the new species discovered by Bechstein himself in the field.

In 1848, looking back over many decades, C.L. Brehm published a harsh critique of Bechstein:

"Bechstein was a friend of my late father and used to live just two hours away from my place of birth. I respected him greatly, but when as a nine-year-old boy I read the erroneous description of the Blackbird's nest he lost all credibility for me. Many other things that I recognized as false in my youth, e.g. the early breeding of the Magpie and the Dipper (both of which were said to build in February), the completely mistaken description of the Kingfisher's nest, and so on, put me off the writings of this great man to such an extent that I simply couldn't read them any longer" (Thomsen & Stresemann 1957: 147).

Stresemann (1951: 296) considered Bechstein's *Gemeinnützige Naturgeschichte* to be "nothing but [....] a rigorously classified collection of material, though unprecedentedly rich in detail". When E. Mey (2003: 70) writes that this judgement is "unjust" since it implies that Bechstein could be "at best regarded as mainly an industrious compiler" then this results from a misunderstanding. An "industrious compiler" is one who brings together already familiar information scattered throughout the literature. But this is not what Stresemann intended. He meant that in its day the *Naturgeschichte* as a collection of facts was unrivalled in its completeness, that is it dealt with the known and many (until then) *unknown* facts regarding the most diverse aspects of birds. But, continues Stresemann, Bechstein – as opposed to Pernau and Zorn – was very reluctant to draw conclusions from these facts and to interpret some of them with regard to their biological significance. See especially Mey (2003, 2010) for a very extensive appraisal of Bechstein.

Biologists (= physiologists) at that time saw themselves (in today's language) as "causation investigators", concerned with the immediate physical-chemical, *functional* (proximate) causes or explanations of biological phenomena (an enterprise that lacked even the fundamental concepts in Bechstein's day), while the physico- or natural theologians emphasized the fitness for purpose (design) of many structures, interpreting them teleologically, so were concerned with their *historical* (ultimate) explanations. As we now know, every biological phenomenon has functional as well as historical explanations, so that an antithesis between the "causation investigators" and the teleologists, as referred to by Stresemann, did not actually exist in retrospect. Yet because of this supposed conflict

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many naturalists around 1800 were reluctant to express their interpretations either in the one direction (functional) or the other (historical). Regarding his explanations of biological structures and avian phenomena, Bechstein might be placed within this group of naturalists.

However, in 1795 the bird-keeper Bechstein suggested in his *Naturgeschichte der Stubenvögel* [English translation of 1838: *The Natural History of Cage Birds*] that individual differences in the quality of song were important in mate choice as he had noticed that female canaries preferred the males with the best voices (Birkhead & van Balen 2008: 285).

Johann Andreas Naumann and Johann Friedrich Naumann (1795–1817). In a 4-volume handbook of the birds of northern Germany, published by Johann Andreas Naumann and his eldest son Johann Friedrich between 1795 and 1803 (with 8 supplements from 1804 to 1817), all species treated are, for the first time, illustrated in a total of 234 outstanding color plates, almost all of them by the younger Naumann, initially in folio and after 1804 in octavo format. The complete title of the work was at first

Ausführliche Beschreibung aller Wald-, Feld- und Wasser-Vögel, *welche sich in den Anhaltinischen Fürstenthümern und einigen umliegenden Gegenden aufhalten und durchziehen*

[***Detailed description of all woodland, field, and water birds*** *which live in and migrate through the Principalities of Anhalt and some surrounding regions*].

With the fourth instalment of the first volume (1797) this title was altered to:

Naturgeschichte der Land- und Wasser-Vögel *des nördlichen Deutschlands und angränzender Länder, nach eignen Erfahrungen entworfen, und nach dem Leben gezeichnet*

[***Natural history of land and water birds*** *of northern Germany and adjacent countries, from our own observations and drawn from life*].

a


Johann Andreas Naumann's
ausführliche
Beschreibung
aller
Wald- Feld- und Wasser-Vögel,
welche sich
in den Anhaltischen Fürstenthümern
und
einigen umliegenden Gegenden
aufhalten und durchziehen.

Ersten Bandes erstes Heft.
Mit 8 Kupfertafeln.

Leipzig, 1795.
Auf Kosten des Verfassers,
und in Commission bey Friedrich Osterloh.

b


Naturgeschichte
der
Land- und Wasser-Vögel
des nördlichen
Deutschlands und angränzender Länder,
nach eignen
Erfahrungen entworfen, und nach dem Leben
gezeichnet
von
Johann Andreas Naumann.

Vierter Band.
Mit Kupfern.

Köthen, 1803.
Auf Kosten des Verfassers,
und in Kommission bei J. A. Aue.

Figs 24a, b. Title pages of J.A. and Johann Friedrich Naumann (1795 [vol. 1, part 1] & 1803 [vol. 4]). Note change of title after vol 1, part 4.

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The physico-theological concept informing Johann Andreas Naumann's study of nature, and of birds in particular, is expressed in the words with which he opened his *Naturgeschichte* (1795–1817):

"From time immemorial, and especially in the present enlightened era, knowledge of fairest nature has been the study that has preached to us of the mighty Creator of the World in his greatness and omnipotence. From the worm to Man, everything reveals to us His omnipotence and greatness. Man would still be too weak, even if he had a thousand tongues, to relate and praise the wonders that surround him in Creation. All the elements praise the glory of the Almighty. The denizens of the air, the birds, are the object with which I intend to entertain my readers and to encourage them in praise of the Almighty" (beginning of the Preface, 1795).

From their earliest youth, his three sons, Johann Friedrich, Carl Andreas, and Gottfried Leberecht accompanied their father on his excursions in the country around Ziebigk near Köthen, learning from him – a "huntsman grown gray in the hunting and trapping of birds" – an intense study of nature and a religiously-founded wonder in all living things. Immediately following the *Naturgeschichte* of Bechstein, the *Naturgeschichte der Land- und Wasser-Vögel des nördlichen Deutschlands* (1795–1817) appeared, with 192 excellent color plates of German birds in folio format, done in the style of the famous bird publications of J.L. Frisch. Almost all plates were by Johann Friedrich Naumann, who was then just 15 years old (he had in fact drawn the first of the illustrations at the age of 14). (Figs. 25a–d). His artistic progress can be observed in the early folio plates. In 1804 the Naumanns changed the plate format from folio to the smaller octavo, so the son engraved all the 192 folio plates again in the smaller format. The species texts in the first two volumes of this *Naturgeschichte* were kept very brief, but the treatment was considerably expanded when Johann Friedrich began to cooperate on their production from volume 3 onwards (as he mentioned in a letter; see Thomsen 1930: 15), though he is credited as co-author on the title page only from the fourth instalment (1803) of volume 4. The texts of the work are based solely on data collected in the field by the Naumanns themselves, and by Naumann senior in his aviary directly adjoining his sitting room. Using these captive birds he was able to calculate the lengths of their migration periods in autumn on the basis of their migratory restlessness, or *Zugunruhe* (1795: 4, 8–9), deducing from his observations that many of them must overwinter in tropical Africa, which was completely unknown at the time (Haffer 2006: 28).

"Adjoining my sitting room I have built a little room on the east side, with a window facing south covered only with wire mesh so that it is open to the air in spring, summer, and autumn, but in the winter a pane of glass is fitted into it. There is a door into my sitting room made only of wire mesh and paper, so that I can let heat into that room when necessary and at the same time can hear what sort of movements the birds are making, day and night, since I have 30 or 40 birds of many different kinds. I keep some to observe their habits, others to hear their attractive song, and others again for use on the trapping ground: in other words I have forest, field, and water birds in there. I can note the exact time of their nocturnal movements because as long as their instinct is active, at night when the moon shines, they fly around in their room, also when the stars are visible in a clear sky" (1795: 4).

"According to my calculation, they can [= summer visitors in autumn] make this journey inside a month; however I have noticed that in their little room the flycatchers and Golden Orioles 'migrate' until the middle of November, because they are restless until that time, but after then become completely still. That Golden Orioles and flycatchers, as well as swallows and other birds, migrate to Africa must be regarded as the truth, since these birds live on insects alone and cannot abide the cold here" (1795: 8–9).

"They [= Golden Orioles] became very restless when the migration period started, flying around in the chamber all night into November. From this one can deduce that this bird migrates a great distance, probably as far as Africa. In February they started their molt and looked a sorry sight. I had to take good care of them because in the past some had died at this time. But as soon as they had come through they grew very lively and started to sing, but in March they were restless again at night" (1795: 196).

"I have often had one of these 'decoy birds' [= Pied Flycatcher] in the chamber and got it used to eating some all-purpose food to keep it alive through the winter, in order to note how long it migrates, and I have found that it is restless until the middle of November, but then becomes quiet again, from which one can conclude that they must migrate just as far as the Golden Oriole" (1797: 203).

Naumann senior reported numerous observations on the behavior of these birds, some of which are given here to illustrate just what an able ornithologist he was.

He wrote on the nest-building of the Golden Oriole (*Oriolus oriolus*): "It is a real pleasure to watch an Oriole building its nest, and I did this often and gladly. Male and female perform this task jointly without being in each other's way. When one of them arrives with a long strand of wool or a dry blade of grass, it attaches first one end of it on the twig with its saliva and then takes the other dangling end and flies with it around the twig, fastening the nest to it so thoroughly that one is unable to detach it without either breaking the twig or tearing the nest apart" (vol. 1, 1797: 195–196).

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a

b

c

d

Figs 25a–d. Four plates from J.A. & J.F. Naumann (1795–1817). 25a: male and female Garganey; 25b: male and female Common Kestrel; 25c: Eurasian Treecreeper (top), Eurasian Nuthatch (center), Wryneck; 25d: Aquatic Warbler, Sedge Warbler (top), Firecrest (center), Winter Wren, Goldcrest. Note also eggs.

A hand-raised Stone-curlew (*Burhinus oedicnemus*) "has become so used to me that it sits at my feet as long as I am in the room. When I enter, the bird approaches me joyfully, lowers its bill towards the floor, spreads its

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wings and tail, and softly calls 'dick, dick, dick'. When it is standing in the sun or in some other comfortable place and someone intereferes with it, then it makes a loud snoring sound to show its displeasure. Its screaming voice is heard only at dusk and dawn. It feeds just as happily at its bowl at night, when a light or the moon is shining, as during the day" (vol. 2, 1799: 74).

In order to discover whether individual Common Buzzards (*Buteo buteo*) – which have very variable plumages – retain their own particular coloration pattern in successive years or molt to a different one, he invented the banding experiment: "In my last years of collecting birds I tried to get to the bottom of this difficult question, so I left alive all those buzzards I caught and fastened a copper ring round their tarsus, on which my name, place of residence, date of capture, and a letter to indicate their plumage type were engraved. Then I set them free hoping to catch them again some time later and perhaps in a different plumage type. Even though I did this with a large number of birds I never again saw a single one of them. All the bands that were sent to me from the neighborhood were from birds I had banded just a short time previously" (vol. 4, 1803: 212; see also Thomsen & Stresemann 1957: 36).

Johann Andreas Naumann rediscovered the fact that long-billed waders are capable of opening only the tip of the bill when necessary (vol. 3, p. XXI, 1799; see also Frisch in his Woodcock account above), and was shocked when this was doubted by a reviewer of his book (supplement 2, 1805: 57). His son was his co-author after volume 3 but was solely responsible for the supplement texts because his father's eyesight had become so bad.

Hybridization of Carrion and Hooded Crows, and the breeding and molting periods of many species are described in the text, as is the separation of pipits and larks – the former dips the tail up and down like the wagtails (1798: 47). The differences between several similar *Acrocephalus* species are outlined, illustrated by Johann Friedrich's magnificent color plates.

Hildebrandt (2007) has done a great service by collecting many faunistically and biologically interesting passages on all the species in the work of the Naumanns, together with a wealth of useful notes and several of J.F. Naumann's color plates, thus making these important publications easily accessible once again.

Species knowledge. The work contains descriptions and illustrations of 285 taxa recognized today as species or subspecies. Those missing in the main text are Wood Warbler, Grey Wagtail, Firecrest, Bearded Reedling, and Penduline Tit, but all are dealt with in the supplementary volumes together with other species. Black and Red Kites are acknowledged as separate species, but Hen, Pallid, and Montagu's Harriers are lumped together under the species name Halbweyhe ["Semi-Harrier"]. The color variants of Common Buzzard are treated as such, and banding experiments are devised to test their constancy (see above). That there is only one species of Blackbird, and not two, is set down here, as well as that there is only one species of Grey Heron. Juvenile *Oidemia nigra* [= *Melanitta nigra*] and *Colymbus septentrionalis* [= *Gavia stellata*] are thought to be species in their own right in the principal text, but this too is corrected in the supplements. Today's *Acrocephalus*, *Sylvia*, and *Phylloscopus* warblers are correctly differentiated. The two *Regulus* species and *Certhia* species are not yet distinguished. Shore Lark, Crag Martin, Water Pipit, Alpine Accentor, Savi's Warbler, Bonelli's Warbler, Collared Flycatcher, Red-breasted Flycatcher, Citril Finch, European Serin, and both choughs are also absent. However the Naumanns were dealing here only with the birds of northern Germany and hence made no great effort at completeness by including species from the south of the country or the Alps. Problems with the reed warblers are discussed in the fourth supplement (1811) and the genus *Acrocephalus* ("pointed head") erected.

Systematics. The classification of birds was once again, as in the *Vogelsteller* of 1789, basically ecological ("*woodland, field, and water birds*") and therefore "old-fashioned", for even Ray (1676, 1678) with Willughby had broken with this tradition and had used structural characters to divide birds into groups. The Naumanns differentiated a total of 30 groups ("Classes") of birds in their geographic region. However, by splitting the pipits from the larks for the first time on the basis of the former's tail-wagging they were employing a behavioral character (very "modern" in this publication) in the systematic classification of a bird grouping. Along the same lines as the Naumanns, Bechstein (1805) later introduced the genus name *Anthus* for the pipits. The following list documents the Naumanns' divisions of the birds of Central Europe, in which the species dealt with in the eight supplements are placed in their appropriate group:

I. *Woodland birds* that have conical bills, eat seeds, and dehusk the seeds: House, Tree, Rock, and Snow Sparrows, Chaffinch, Brambling, Greenfinch, Linnet, Twite.

II. *Woodland birds* that have conical bills with pointed tips, though not circular in cross-section but vertically flattened; forage on trees and tall plants, hanging with sharp claws on seed-heads: Goldfinch, Siskin, Redpoll.

III. *Thick-billed birds* that forage in trees but also walk and hop: Hawfinch, Pine Grosbeak, Bullfinch, Common Crossbill, Parrot Crossbill, Common Rosefinch.

IV. *Buntings*, upper mandible with ridges in the hard palate and smaller than the lower mandible. Seeds are cut in the bill and dehusked. Usually walk but sometimes hop: Corn,

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Reed, Lapland, and Snow Buntings, Yellowhammer, Ortolan, Dunnock.

V. *Pigeons and doves*: Wood Pigeon, Stock Dove, Turtle Dove.

VI. *Woodland game-birds*: short, curved bill, feed on buds, plants, berries, larvae, worms, etc, seeds; walk and never hop: Capercaillie, Black Grouse, Hazel Grouse, Pheasant.

VII. *Woodland birds* that feed on insects and larvae etc. in trees, also seeds. Bill small, hard, wedge-shaped, claws sharp for climbing and hanging, always hop. Useful birds that eat many insect pests and their eggs: Great, Blue, Azure, Marsh, Crested, Long-tailed, and Penduline Tits, Bearded Reedling.

VIII. *Woodpeckers*: Black, Green, Grey-headed, Greater Spotted, Middle Spotted, Lesser Spotted, White-backed, and Three-toed Woodpeckers, Wryneck, Nuthatch, Wallcreeper, and treecreeper.

IX. *Juniper birds*: hop, like to eat juniper berries: Mistle, Song, and Rock Thrushes, Dusky Thrush (subspecies *eunomus*), Fieldfare, Redwing, Blackbird, Ring Ouzel, Waxwing.

X. *Woodland birds* that feed on insects, larvae, worms, etc. and berries: Barred and Garden Warblers, Blackcap, Common Whitethroat, Lesser Whitethroat, Willow and Wood Warblers, Chiffchaff, Nightingale, Thrush Nightingale, Robin, Bluethroat, Common and Black Redstarts.

XI. *Woodland birds* that live on earthworms and insects, bill elongated and pointed, walk on the ground (do not hop): Common Starling, Rosy Starling, Hoopoe, Bee-eater, Grey, Yellow, and Pied/White Wagtails.

XII. *Woodland birds*, flycatchers and berry eaters, bill pointed and broad at the base. They sit still and wait for prey: Golden Oriole, Icterine Warbler, Spotted Flycatcher, Pied Flycatcher.

XIII. *Swallows*, bill broad, catch their prey in flight: Common Swift, House and Sand Martins, Barn Swallow, Nightjar.

XIV. *Woodland birds* that eat only worms, larvae, insects, etc., but not berries; hop only: Cuckoo, Great and Eurasian Reed Warblers, Marsh, Aquatic, Sedge, River, and Grasshopper Warblers, Wren, Fire-/Goldcrest, Northern Wheatear, Whinchat, Stonechat.

XV. *Game-birds*, eat seeds, green plants, worms, larvae, etc., never perch in trees: Great Bustard, Macqueen's Bustard, Common Crane, Black-bellied Sandgrouse, Grey Partridge, Ptarmigan, Quail, Corn Crake, Collared Pratincole.

XVI. *Larks*, farmland birds that feed on seeds, green shoots of crops and other plants, with small hard bills. Walk rather slowly: Sky, Wood, and Crested Larks, Snow Bunting.

XVII. *Larks with thin bills*, feed on worms, insects, etc., not seeds, move their tails like a wagtail; they form a transition from the larks to the wagtails: Tawny, Meadow, and Tree Pipits.

XVIII. *Farmland birds that are snipe-like*, walk slowly: Curlew, Golden Plover, Dotterel.

XIX. *Plovers*, form a transition from curlews to snipes and sandpipers: Lapwing, Grey Plover, Turnstone, Common Ringed/Little Ringed Plover.

XX. *Snipes*, bill long, soft, pliable, bill tip can be opened separately: Eurasian Woodcock, Great, Common, and Jack Snipes.

XXI. *Water snipes* [waders], long-legged, walk slowly: Curlew, Bar-tailed Godwit, Greenshank, Spotted Redshank, Common Redshank, Black-tailed Godwit, Black-winged Stilt, Ruff, Red Knot, Sanderling, [*Schwarzbrauner Sandläufer*] Wood Sandpiper?, Marsh, Curlew, Green, Common, and Broad-billed Sandpipers, Dunlin, Little Stint, Red-necked Phalarope.

XXII. *Herons and storks*: White and Black Storks, Grey, Purple, Night, and Squacco Herons, Great White Egret, Little Egret, Spoonbill, Eurasian Bittern, Little Bittern, Glossy Ibis.

XXIII. *Waterhens*, feed on water plants and water insects: Moorhen, Coot, Water Rail, Spotted Crake, Little/Baillon's Crake.

XXIV. *Gulls and terns*: Black-headed, Little, Common, Glaucous, and Lesser Black-backed Gulls, [*Kleine bunte Meve*?], Kittiwake, Arctic Skua, Caspian, Common, Little, and Black Terns. In supplements: White Pelican, Great Cormorant, Northern Gannet.

XXV. *Swans, geese, and ducks*: Mute Swan, Whooper Swan, Common and Ruddy Shelducks, Grey, Bean, Brent, White-fronted, Snow, and Barnacle Geese, Mallard, Gadwall, Garganey, Eurasian Teal, Shoveler, Wigeon, Pin-

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tail, Long-tailed Duck, Harlequin Duck, [*Große Tauchente*] Goosander/Red-breasted Merganser ?, Common Eider, Goldeneye, Tufted Duck, Pochard, Ferruginous Duck, Greater Scaup, Common and Velvet Scoters, Red-crested Pochard, Goosander, Red-breasted Merganser, Smew.

XXVI. "*Divers*": Common Guillemot, Black Guillemot, Puffin, Little Auk, [*Gesprenkelter Seetaucher*] Yellow-billed Loon ?, Great Northern, Red-throated, and Black-throated Loons, Great Crested, Red-necked, Black-necked, and Little Grebes, [*Schwarzbrauner Taucher*] Slavonian Grebe ?, Kingfisher, Dipper.

XXVII. "*Semi-raptors*": Raven and crows: Common Raven, Carrion and Hooded Crows, Rook, Western Jackdaw, Magpie, Eurasian Jay, Nutcracker, European Roller.

XXVIII. *Shrikes*: Transition species from semi-raptors to the raptors proper. Great Grey, Lesser Grey, Woodchat, and Red-backed Shrikes.

XXIX. *Raptors*: Black Vulture, Griffon Vulture, [*Gemeiner Adler*] Black Kite ?, White-tailed, Golden, Short-toed, and Lesser Spotted Eagles, Osprey, Gyrfalcon, Saker, Peregrine, and Red-footed Falcons, [*Blaufalke*?], Hobby, Merlin, Common Kestrel, Goshawk, Sparrowhawk, [Halbweyhe = Hen, Montagu's, and Pallid Harriers], Marsh Harrier, Red Kite, Common, Rough-legged, and Honey Buzzards, [*Eulenfalke*?].

XXX. *Owls*: Eagle, Snowy, Long-eared, Scops, Short-eared, Tawny, Barn, Little, Tengmalm's, Pygmy, Ural, and Hawk Owls.

Friedrich Tiedemann (1810, 1814). The first textbook of general ornithology after J. H. Zorn's *Petino-Theologie* (1742–1743) was written by Friedrich Tiedemann, Professor of Anatomy and Physiology at the universities of Landshut and, from 1816, Heidelberg. He published major works on the anatomy of fish, reptiles, amphibians, and birds, later working on the physiology of the digestive system of mammals. He was no field ornithologist, but at the start of his career he brought out a detailed *Anatomie und Naturgeschichte der Vögel* (1810, 1814) [*Anatomy and natural history of birds*] in two volumes as part of an unfinished zoological textbook. The first volume on the anatomy of birds was based on his own extensive studies, the second was a detailed representation of the life and distribution of birds gleaned from all of the German and international literature ("Reproduction and growth", "Metamorphosis of birds", "Occurrence and distribution", and "Movements of birds"). In this work Tiedemann quoted widely from the contributions to the natural history of birds, nests, nest building, etc. by Zorn, Derham, and other 18th-century physico-theologians, and also included much from recent ornithological literature on European and tropical birds (Stresemann 1951: 297–303).

Like Zorn 70 years before, Tiedemann described the purposiveness (*Zweckmäßigkeit*) of avian body structures, concluding that "the entire anatomy of the bird is organized for flight. The head is small, light, and ends in a more or less pointed bill, a form that makes cutting through the air very much easier" (p. 348). During flight the wings act like paddles, sails, or parachutes, the tail like the rudder of a ship. A muscle contracts the toes when the knee joint is flexed thereby fastening the sleeping bird to the branch. "When sleeping, birds mostly put the head under one wing, so that the line of the center of gravity passes between the feet" (p. 365).

Birds breed once or several times in spring, earlier in southern Europe than farther north, but the crossbill breeds in winter and tropical birds have completely different breeding periods. Many males have a breeding plumage, sing, and perform a courtship display. Nest types, sites, and construction are described, as are tropical communal nests. The form of the nests of Dipper, Wren, and Long-tailed Tit are presented, using the descriptions of Zorn, Derham, and Bechstein. The nest-building instinct is innate: "We must suppose that birds are driven by a blind, innate compulsion and determination to build their nests, but to explain this is still outside the compass of our knowledge" (p. 60; with reference to H.S. Reimarus 1760). Tiedemann knew that smaller birds in South America lay fewer eggs (2 to a maximum of 4) than those in Europe, and that young females lay fewer eggs than older ones of the same species. Birds that breed several times in a year lay fewer eggs in later clutches than in the first clutch. "The degree of development of birds at hatching depends on their way of life and where they live" (p. 75). Ground-nesting species have relatively large eggs and the young are relatively advanced in their development at hatching, while the young that remain long in the nest are born naked and helpless. The "shape of eggs before incubation" and "malformed eggs" are discussed, and the section "On breeding" supplies information on the respective share in incubation of females and males. The (designed, since protective) covering of the eggs when temporarily leaving the nest was well known to the author from Moorhen, Capercaillie, ducks, geese, and swans, as was the similarly purposive "distracting" display in species with an open nest (after Zorn). The varying number of eggs in the nest of different species and the differing incubation periods are illustrated in tables (pp. 63–72 and 138–139). The length of incubation depends on the stage of development the young are in on hatching, hence that of nidicolous songbirds is relatively short, that of nidifugous species relatively long.

The section on the "Metamorphosis of birds" from hatching to death deals with the rearing of young by their

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parents, growth, molt, song development, etc.: "Young birds learn [….] the actual song successively, mostly through imitation of the song of their parents. [….] When young songbirds are removed from their parents they can easily learn the song of other birds with which they might come together" (pp. 288–289). Juvenile plumage often resembles that of females; molting waterbirds "often lose all their flight feathers simultaneously, so have to hide themselves in the reeds", and the color of the winter plumage of many birds is often quite different from the color in spring; diurnal rhythm (singing and foraging in the morning, going to roost at twilight).

Morphological adaptations "designed for purpose" in birds are explained by the influence of climate, especially temperature (p. 567): in northern realms, for protection against cold, birds have a thick covering of feathers rich in down, which also covers the feet. Birds in the tropics have less feathers and a lighter plumage, but there can be luxurious feather growth in particular parts of the body (e.g. the long "tail" feathers of peacocks, pheasants, and birds of paradise). Feather coloration in the far north is often white, gray, brown, or black, in lower latitudes however there is a dominance of lively and frequently iridescent colors.

After a long discussion regarding the global distribution of birds, Tiedemann's conclusion was that "through its structure and formation, according to its own particular climatic and physical conditions, each part of the Earth has brought forth its own particular forms of plants and animals" (p. 566). Therefore in any particular area the distribution of birds depends on its plant and animal production (Mauersberger 1980: 11). Tiedemann ends his work (1814) with a long bibliography of ornithological literature from each country and a discussion of the movements and migration of birds in Europe/North Africa, Asia, North America, and the southern hemisphere.

No other author in the 19th century attempted again to write such a general study of ornithology, bringing the great variety of aspects concerned together under overall headings, as Erwin Stresemann was to do so brilliantly over a hundred years later in his handbook *Aves* (1927–1934). When examining Tiedemann's explanations of many facts we must distinguish between the *functional* and *historical explanations* that underlie every biological phenomenon (Mayr 1982). The emergence of the "*zweckmäßige* [adaptive/purposive] bark-coloration" in the plumage of Wryneck and treecreepers in the course of evolution, as well as the camouflage colors of ground-breeding species and their "protective effect", is explained today by natural selection, while according to the 18th century physico-theologians such phenomena were simply seen as due to the wisdom and goodness of the Creator. These are the historical, evolutionary-biological (ultimate) explanations of the development of such plumage colors. Their functional, immediate (proximate) explanations are to be found in the basic physiological processes controlling the differentiation of feather pigmentation and its deposition on the growing feather. Similarly, there are certain physiological hormonal reasons why a migratory bird should begin its journey on a particular autumn night (functional explanation), but the historical one of why it has to leave its breeding site and migrate to different winter quarters at all lies in its "genetic program", which has developed through natural selection in the course of evolution.

In many cases Tiedemann discussed the "fittedness" of avian structures (historical explanations) without using the terms adaptedness or purposiveness, such as the streamlined form of the body as an adaptation to flight, the automatic clasping of the toes of arboreal species when the knee joint is bent, and so on. In other cases he speaks as a physiologist and tries to find functional reasons for certain phenomena, without attempting to consider possible historical explanations for these cases. His functional explanations were bound to fail because knowledge of the entire physiological-chemical foundation of biological phenomena was completely inadequate at the time. Stresemann (1951: 302–303) quotes several such examples from Tiedemann's book (1814, pp. 14, 72–73, 541, 572, 594, 597–599), though without emphasizing the important difference between functional and historical explanations. For example, Tiedemann looked for the origin of the differing sizes of clutches among birds in their diet (smaller number of eggs with animal food, larger number with vegetable food; functional explanation), and Stresemann accused him of ignoring the biologically determined greater or lesser reproduction requirement of the various species (historical explanation). Tiedemann further believed that plumage color was determined by diet and temperature (carbon in its multifarious degrees of oxidation and the ambient temperature; functional causes), while Stresemann remarked, "That plumage coloration in many cases could be related to the necessity of a bird to protect itself (Zorn 1742) is not even considered by our physiologist" (p. 302; historical cause). For the biologists – who were mostly physiologists – working around the year 1800 there was no alternative to a physical cause for traits, since for them the teleological (historical) explanation of adaptations by the physico-theologians was no explanation at all. It was only evolutionary biology grounded on natural selection that made an understanding of adaptedness in nature possible. But Tiedemann and his contemporaries had not yet reached that level of thinking, although he himself had very concrete ideas on the evolution of animals. When he wrote that "With every great upheaval of the Earth animals have become extinct, as the bones of mammoths, the *Ohiothiere* [mastodons], the *Paläotherian* [horse- or tapir-like mammals], the *Anoplotherian* [pig- or cow-like mammals], the *Megatherian*, the *Megalonix* [two giant ground sloths], the *Ornithocephalus* [a genus

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of pterosaur] and many other animals conclusively prove. But after each such upheaval it seems that new animals have been created, presumably mainly via gradual metamorphosis and alteration of the older animals that had survived into new animal forms, effected by new climatic and physical influences" (p. 322); " …… species are subject to metamorphosis over time just as individuals are" (1814: 325).

(6.) The "Golden Age" of field ornithology (1820–1850)

After 1750 and into the 19th century there was in Europe a fairly large number of breeding birds that are now rare, e.g. Short-toed Eagle (*Circaetus gallicus*), Ruff (*Philomachus pugnax*), Great Snipe (*Gallinago media*), Gull-billed Tern (*Gelochelidon nilotica*), Stone-curlew (*Burhinus oedicnemus*), European Roller (*Garrulus glandarius*), Eurasian Hoopoe (*Epupa epops*), Rock Thrush (*Monticola saxatilis*), and Aquatic Warbler (*Acrocephalus paludicola*). They inhabited the so-called common or unenclosed land. This comprised a wide variety of landscapes, ranging from gravel beds, impoverished grassland and heathlands, moors and bogs, riverine forest, and open woodland, accounting for approximately two-thirds of the area of Central Europe and characterizing the appearance of the countryside at that time. What remains of these habitats today are mere remnants representing a small fraction of the original (Schulze-Hagen 2005).

During the period 1820–1850 several ornithologists were in contact with each other internationally, working on a set of productive questions. They, for the first time, constituted a discipline of ornithology (Farber 1982).

Johann Friedrich Naumann (1780–1857) (Fig. 26). The "Golden Age" (1820–1850) of Central European field ornithology wintnessed the appearance of the outstanding works of Johann Friedrich Naumann (1820–1844, 1860), Christian Ludwig Brehm (1820–1822, 1823–1824, 1831), and Frederik (Friderich) Faber (1822, 1824–1827, 1825–1826). These publications laid the ground for future research in the coming decades. The 1820s heralded a first great flowering of field ornithology in Germany.

Naumann's 12-volume *Naturgeschichte der Vögel Deutschlands* (1820–1844, with addenda 1844–1854 and a supplementary volume in 1860) [*Natural history of the birds of Germany*] was the titanic labor of one man that served later generations as a handbook on the life and habits of European birds (Fig. 27). For his names, see online Appendix 3. Praise for the *Naturgeschichte* by two great 19th-century British ornithologists was all but boundless:

"[B]y far the most important work of this or any other period was the publication of Naumann's 'Birds of Germany', which was commenced in 1820 and completed in 1844. Twelve octavo volumes of about 600 pages each testify to the industry of the author, whilst a careful study of the content proves him to have possessed a knowledge of the various plumages of the birds of which he treats, their habits, songs, call-notes, food, and all the numerous details of their history, which a lifetime devoted to their observation was able to teach, not only unrivalled by any author before or since, but far above and beyond all hope of rivalry [...] Had this work only been translated into English, half the nonsense that subsequent ornithologists have written on birds would never have appeared (Henry Seebohm 1885: XII). *"This Naturgeschichte der Vögel Deutschlands, being almost wholly re-written by his son J.F. Naumann, is by far the best thing of the kind as yet produced in any country. The fulness and accuracy of the text, combined with the neat beauty of its coloured plates, have gone far to promote the study of Ornithology in Germany"* (Alfred Newton 1896: 17), *and "for fulness of treatment, perspicuity, and general accuracy, the work of Johann Friedrich Nauman has not been surpassed* (Alfred Newton 1905: 37; see also Thomsen & Stresemann 1957: 180–181).

Fig. 26. Portrait of J.F. Naumann (from Thomsen & Stresemann 1957).

In a manner of speaking, Naumann senior had got his son Johann Friedrich off to a flying start by introducing him to ornithology at the tender age of 8 or 9 years old, passing on all his accumulated wisdom and enabling the young man to build on an already substantial foundation. In great

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Johann Andreas Naumann's,
mehrerer gelehrten Gesellschaften Mitgliede,
Naturgeschichte
der
Vögel Deutschlands,
nach
eigenen Erfahrungen entworfen.
Durchaus
umgearbeitet, systematisch geordnet, sehr vermehrt, vervollständigt, und mit getreu nach der Natur eigenhändig gezeichneten und gestochenen Abbildungen aller deutschen Vögel, nebst ihren Hauptverschiedenheiten, aufs Neue herausgegeben
von
dessen Sohne
Johann Friedrich Naumann,
der naturforschenden Gesellschaft zu Halle; der Societät für Forst- und Jagdkunde zu Waltershausen und Dreyßigacker; der Wetterauischen Gesellschaft für die gesammte Naturkunde zu Hanau; der Gesellschaft für die gesammten Naturwissenschaften zu Marburg; der Leipziger naturforschenden Gesellschaft, wirklichem und correspondirendem Mitgliede, und der allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften Ehrenmitgliede.
Erster Theil.
Mit 48 colorirten und 2 schwarzen Kupfern.
Leipzig, bei Gerhard Fleischer.
1820.
Bibliothek des Kgl. Zoolog. Museums Berlin

Fig. 27. Title page of J.F. Naumann, volume 1 (1820).

detail, the voluminous text of the *Naturgeschichte* deals with the name, synonyms, description, occurrence, habits, diet, breeding, predators, hunting, and beneficial and harmful effects for every species. This pattern in describing bird species was probably taken by Naumann from Blasius Merrem (Thomsen & Stresemann 1957: 93). The anatomist C.L. Nitzsch, and after his death R. Wagner, helped with contributions on the anatomy of the various families dealt with in individual volumes. In the foreword to the second volume in 1822, Naumann discusses the, for him, unbridgeable opposition between the representatives of the two great branches of ornithology: the field ornithologists and the systematists, criticizing the continual changes being made to the "artificial construction" that is avian systematics:

"Everyone thinks they can have a try, and if someone has seen a couple of hundred mounted birds then he wants to be a reformer and improve the system.—Go out into the field, see the animals in their lives and habits; how different then will you judge when you have found that things are not what they appeared to be in the cabinet [.....] It has always seemed to me that the intellectual and scholarly philosopher of nature [= systematist] cannot be reconciled with the son of nature [= field ornithologist] who simply follows the straight path that nature has marked for him.—Whoever has made it his aim not just to hunt birds for his collection but also to observe them in their haunts and in their ways, and to study their habits in nature, will find as much pleasure in this as work and will have little time left to occupy himself with the scribblings of the creators of systems" (1822: I–II).

The way of life of birds. The focus of Naumann's work lay in the portrayal of the way of life of birds, which he described with affection and in great detail. Habitat preference, diet, nesting habits, and relationship to their surroundings are minutely discussed, but there is little trace of the earlier theoretical impulses of J.H. Zorn or F. Faber in Naumann's approach, which is more painstaking observation than causal research (Mauersberger 1980). The competitive relationships between several species is again something that Naumann appears uninterested in. Nevertheless, there are the beginnings of a causal outlook in areas of ecology in some of Naumann's findings, e.g. the relation between diet and foraging method. Habitat preference can be discerned in Naumann's texts and foraging sites are clearly recognizable (tall herbs, treetops, ground), as are the composition of the diet, nest site, nest material, and the many different ways of movement and forms of behavior in birds.

Illustrations. The birds in the *Naturgeschichte* are illustrated on a total of 391 excellent hand-colored copperplates, 379 of which are by J.F. Naumann and which he engraved anew for this work as well as making many improvements in their drawing compared with earlier versions. The additional 12 plates in the supplementary volume of 1860 are by F. Sturm (see *Neuer Naumann*, Vol.1, p. XXV, 1897). Naumann achieved a high degree of perfection, especially in his treatment of plumages, so that his plates are counted among "the most lifelike and accurate representations of birds ever made" (Nissen 1953, 1957). However Naumann's paintings – of raptors in particular – were the subject of some critical remarks by one contemporary ornithologist. Hermann Schlegel (1849) in Leiden, who had himself published large-format illustrated books, wrote:

"Among the older German artists, Johann Friedrich Naumann and Susemihl deserve special mention. The former has managed, through long and careful study of the living bird, to produce small, often very characteristic, painstaking illustrations, but they reveal the hand of the naturalist rather than the artist. They are usually lacking in spirit, liveliness, and elegance. The engraving is mostly hard and unsure, the embellishments meager; all in all even the drawing, with the exception of the waterbirds, marshbirds, and songbirds, leaves much to be desired, and not infrequently is quite disfigured by Naumann's habit of drawing the eyes much larger than they are in nature. This

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is especially the case in his birds of prey, which (as in most works) leave the most to be desired, and often are even less than mediocre."

Ludwig (2000: 101) saw the reason for the stiff representation of the raptors in the fact that Naumann had only "limited artistic ambitions, stuck to traditional patterns of illustration, and did not develop his own pictorial forms corresponding to his demands. He did not present birds as if he were drawing living creatures moving through their environment but mounted specimens on their pedestals placed before white walls". While it is actually the case that in these instances Naumann had indeed created plates for ornithologists, and not as an artist, Schlegel had specifically excluded Naumann's plates of waterbirds, marshbirds, and songbirds from this criticism. Here the birds appear as living creatures, and their habitat is often suggested in the background. On the whole Naumann's bird paintings are evidently illustrations for his scientific *Naturgeschichte* and not works of art in their own right.

New Descriptions. In the course of their efforts to exactly differentiate the species and subspecies of birds, father and son Naumann (later Johann Friedrich alone) described a host of new forms, and gave them scientific names. Some of these names have retained their validity while others have failed to gain permanent recognition. Later work showed that many of them referred to already known species or subspecies[10]:

Cygnus xanthorinus J. F. Naumann, 1842 [= *C. c. cygnus* (L.), Whooper Swan]
Cygnus melanorhinus J. F. Naumann, 1842 [= *C. bewickii* Yarrell */columbianus*, Bewick's Swan]
Anser intermedius J. F. Naumann, 1842 [= *A. albifrons flavirostris* Dalgety & Scott, 1948[11], Greenland White-fronted Goose]
Anser minutus J. F. Naumann, 1842 [= *A. erythropus* (L.), Lesser White-fronted Goose]
Anas leucopis J. F. Naumann, 1799 [= *Aythya nyroca* (L.), Ferruginous Duck]
Anas merganser J. F. Naumann, 1799 [= *Alopochen aegyptiaca* (L.), Egyptian Goose]
Buteo leucurus J. F. Naumann, 1853 [= *B. r. rufinus* (Cretzschmar), Long-legged Buzzard]
Limosa baueri J. F. Naumann, 1836 [= *L. lapponica* ***baueri*** Naumann, 1836, Bar-tailed Godwit]
Tringa macroura J. A. & J. F. Naumann, 1811 [= *Bartramia longicauda* (Bechstein, 1812), Upland Sandpiper]
Scolopax Glottis minor J. A. Naumann, 1799 [= *Tringa stagnatilis* (Bechstein, 1803), Marsh Sandpiper]
Phalaropus angustirostris J. F. Naumann, 1836 [= *Ph. lobatus* (L.), Red-necked Phalarope]
Mormon [= Fratercula] **corniculata** J. F. Naumann, 1821, Horned Puffin]
Larus ***glaucescens*** J. F. Naumann, 1840, Glaucous-winged Gull
Larus cachinnans ***michahellis*** J. F. Naumann, 1840 [= *Larus* ***michahellis*** J. F. Naumann, 1840, Yellow-legged Gull
Sterna macrura J. F. Naumann, 1819 [= *S. paradisaea* Pontoppidan, 1763, Arctic Tern]
Sterna fluviatilis J. F. Naumann, 1819 [= *S. h. hirundo* L., Common Tern]
Acrocephalus lacustris J. F. Naumann, 1811 [= *A. a. arundinaceus* (L.), Great Reed Warbler]
Acrocephalus stagnatilis J. F. Naumann, 1811 [= *Locustella fluviatilis* (Wolf, 1810), River Warbler]
Sylvia (Calamoherpe) horticula J. F. Naumann, 1853 [= *Acrocephalus s. scirpaceus* (Hermann, 1804), Eurasian Reed Warbler]
Sylvia cariceti J. F. Naumann, 1821 [= *Acrocephalus paludicola* (Vieillot, 1817), Aquatic Warbler]
Sylvia ruficapilla J. F. Naumann, 1853 [= *S. a. atricapilla* (L.), Blackcap]
Troglodytes musculus J. F. Naumann, 1823 [= *T. aedon* ***musculus*** Naumann, 1823, Southern House Wren]
Troglodytes stellaris J. F. Naumann, 1823 [= *Cistothorus platensis* ***stellaris*** Naumann, 1823, Sedge Wren]
Troglodytes Bechsteinii J. F. Naumann, 1822 [= *T. ruficollis atrogularis* Jarocki, 1819, Rufous-browed Wren]

The Naumanns described the Upland Sandpiper under the name *Tringa macroura* from a bird that had been collected as a "vagrant" on the River Werra in Hessen and sent to Herr von Minckwitz in Silesia (see Nachtrag 5: 274, 1811). J.F. Naumann very likely examined and sketched the specimen during his visit there in 1805. The mounted Horned Puffin that Naumann used in his initial description of the species was among a collection of seabirds "from the waters around Kamchatka" that he had received from Peter von Wöldicke (Brunsbüttel) and that most probably had been obtained during the Russian expedition of 1815–1818 (Hildebrandt 2001: 39). The Glaucous-winged Gull was described by Naumann from North American specimens in the Berlin Zoological Museum in the 10th volume of his *Naturgeschichte* in 1840.

Naumann brought three skins of a laughing-dove-type columbid from Turkey home with him from his trip to Hungary in 1835. He had noticed them in the National Museum in Budapest and sent a description and colored illustration of the bird to his Hungarian acquaintance E. von Frivaldsky, who used both of them in his publication (1838) on the Collared Dove under the name *Columba risoria* var. *decaocto* Friv. (Stresemann 1953; Thomsen & Stresemann 1957: 126–127).

A series of bird species and subspecies were named by contemporaries or later ornithologists in J.F. Naumann's

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honor. Some remain valid, while others were synonymized:
Fratercula arctica ***naumanni*** Norton, 1901, Atlantic Puffin
Falco ***naumanni*** Fleischer, 1818, Lesser Kestrel
Turdus ***naumanni*** Temminck, 1820, Naumann's Thrush
Gallinula naumanni Schinz, 1821 [= *Porzana pusilla intermedia* (Hermann), Baillon's Crake
Acridotheres tristis ***naumanni*** Dementiev, 1958, Common Myna
Sylvia naumanni Müller, 1851 [= *S. a. atricapilla* (L.), Blackcap]
Troglodytes naumanni Brehm, 1855 [= *T. t. troglodytes* (L.), Winter Wren]

"The Naumann Cult". The more substantial books dealing with the avifauna of Germany which appeared in the latter half of the 19th century were all more or less extracts from "Naumann". Many ornithologists were convinced that almost everything worth knowing about Germany's birds was now available: "Because of the smooth polish of the descriptions, [Naumann's *Naturgeschichte*] had more of an instructing than a stimulating effect" (Stresemann 1951: 314, 352). Even Altum's interesting ideas in his book *Der Vogel und sein Leben* (1868) [*The bird and its life*] on the impact of instincts in the life of birds found no resonance among his colleagues. Thus an uncritical "Naumann cult" (Heinroth 1917) had arisen among ornithologists which put a brake on progress in the discipline and culminated in a new edition of Naumann's *Naturgeschichte* (1897–1905) in 12 folio volumes, with new illustrations by a variety of artists. The copper plates of Naumann's bird paintings were no longer extant so new originals had to be commissioned from a series of artists. His text was reprinted but many passages, mostly regarding faunistics, were inserted. This new edition was subject to considerable criticism from various sides, but, as Hartert wrote (1930: 4): "One can be as critical as one likes about the so-called 'New *Naumann*' (and there is indeed much in it to criticize!) but it must be admitted that it has made Naumann's name better known than ever before and has reached many more hands than the 'Old *Naumann*' would ever have done."

Also the printing quality of the *New Naumann* was attacked, as the following example from more recent years illustrates:

"As a bibliophilic enterprise this edition fails in every category. Printing quality, typography, print area, everything shows a dreadfully low level of taste. Although excellent work has been done by artists like Otto Kleinschmidt, Anton Göring, J. Keulemanns, Stephan von Necsey, Bruno Geisler, Oskar von Riesenthal, and E. van Maes, the colors of the chromolithographic plates are blatantly overdone and strive only for noisy effect" (Marholz 1965: 384).

Schalow (1909) presents an interesting survey of Naumann's status and the research prompted by his work. In 1930, on the 150th anniversary of Naumann's birth, L. Schuster, E. Hartert, O. Heinroth, L. von Boxberger, O. Kleinschmidt, and O. Reiser honored his achievements from a number of different perspectives in the journal *Beiträge zur Fortpflanzungsbiologie der Vögel* (Vol. 6: 1–9), but also pointed out various shortcomings in his work, such as the "simply invented" incubation periods for many species. "Naumann gives a nicely rounded off account for almost every bird and admits no gaps in his observational knowledge, since how else could he manage to claim that the completely naked nestling of the Black Woodpecker was covered in down?", asked Heinroth (1930: 5). It was he who "finally helped [ornithological progress] in Germany to breach the wall erected by the Naumann cult" (Stresemann 1951: 352), mainly through the weighty 4-volume work by him and his wife on *Die Vögel Mitteleuropas in allen Lebens- und Entwicklungsstufen photographisch aufgenommen und in ihrem Seelenleben bei der Aufzucht vom Ei ab beobachtet* (1924–1933) [*The birds of Central Europe photographed in every stage of life and development and observed in their behavior from the egg onward*], which contained much new material on the biology of the European birds that he raised together with his wife Magdalena. Heinroth's (1917) critique of some statements in Naumann's work does little to damage its reputation; the author of a publication of such magnitude inevitably suffers the fate of a few errors here and there in its volumes:

"He did not notice the voice differences beween the sexes in ducks and did not believe that the young Cuckoo ejected its fellow nestlings from the nest. As was generally believed in his day, he ascribed conscious action to birds."

Even the young G. Stein (1928: 129) dared to find fault with Naumann: his account of the breeding biology of the Common Sandpiper "must be regarded as erroneous in its most important points", he wrote.

In a historical essay dealing with statements on the incubation periods in a series of bird species in the works of past ornithological authors, Margaret Nice (1954) showed that certain false assertions have been repeated in the literature from Aristotle right down to the present day (see Table 2, Haffer 2006: 36). The duration of incubation was underestimated by many early authors, especially in raptors and some marshbirds, the mistaken assumption being that they assumed that the body size of a bird or volume of its egg were the important determining factors. While these parameters do determine the length of the incubation time to some extent, there is considerable variation in different avian families. Zorn (1742) gave some correct information concerning incubation based on

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his own field observations, but they remained unregarded by later authors. Bechstein and the Naumanns estimated incubation duration in many species on the basis of body size, and they were mostly wrong. Only since the publications of Heinroth and Niethammer have correct incubation times been given for the majority of species. Of the 11 incubation durations given by Heinroth (1922) all are correct, while of the 15 set down in Niethammer's *Handbuch* (1937–1942) only that of Black Tern (*Chlidonias niger*) is mistaken (14–17 instead of the correct 20–22 days).

Christian Ludwig Brehm (1787–1864)

"Old Brehm", a Protestant parson in Renthendorf (Thüringen), was a late physico-theologian (Fig. 28). The study of nature, and of birds in particular, was for him "a true divine service", allowing him to see "the infinite wisdom of the Almighty even in insignificant and seemingly chaotic things". "The naturalist must follow the Creator and try to recognize His footsteps everywhere. The more pious our heart, the more will the veil be lifted that hides the Works of God from our feeble eyes" (Brehm 1827).

Like his fellow divine J.H. Zorn one hundred years earlier, Brehm was a teleologist who everywhere saw "the most perfect expressions of Purpose". He asserted that "Every creature is fitted in every way to the place in which it lives, and for the food that it eats […] In cold countries plumages are thicker than in warm climes. The Ptarmigan that live in the north and in the Alps are yellow, brown and black in the summer, like the rocks among which they live, and white in the winter". He compared the details of the climbing apparatus of the Nuthatch and the woodpeckers (1822, 1827; see Stresemann 1951: 305–306). Hence Brehm became, like Zorn before him, a pioneer of functional or biological morphology, in that he studied the adaptations of birds to their environmental conditions. His 3-volume *Beiträge zur Vogelkunde* (1820–1822) [*Contributions to ornithology*] had a lasting influence on the course of the young discipline. Thanks to his extensive collection of skins – around 9000 specimens at the end of his life – he was able to study molt, juvenile and adult plumages, and individual variations in many species. Brehm edited the first ornithological journal, *Ornis, oder das Neueste und Wichtigste der Vogelkunde* (1824–1827) [*Ornis, or the latest and most important information on ornithology*], but it ceased publication after only three issues.

As an ornithologist Brehm was a meticulous observer. For example he demonstrated that birds could simultaneously be good biological species and morphologically very similar (sibling species), such as Common and Short-toed Treecreepers, Marsh and Willow Tits, Firecrest and Goldcrest, or Crested and Thekla Larks. Despite considerable opposition from several colleagues he insisted that these birds belonged to separate biological species and occurred

Fig. 28. Portrait of C.L. Brehm (from Haffer 2001; Brehm-Gedenkstätte, Renthendorf, Thüringen).

sympatrically without interbreeding. He was eventually proved right, although it would take more than half a century until the last skeptics admitted that the two treecreepers and the two tit species each belonged to different species. Common Nightingale and Thrush Nightingale (Sprosser) had been known to naturalists as separate species since the time of J.L. Frisch (1733), when it was also realized that the very similar leaf warblers (*Phylloscopus*) as well as the dark-colored flycatchers (*Ficedula*) should probably be split into different species.

During the 1820s and 1830s Brehm assumed that each one of his morphospecies – European Robin, Common Chaffinch, Common Redstart, etc. – represented biological entities whose subspecies replaced each other to create in each case a geographical-ecological mosaic. Since he believed (in contrast to most of his contemporaries and to us today) that along their contact zones these subspecies *did not* interbreed, he treated his subspecies as (in today's language) parapatric species, and most of his morphospecies as *Artenkreise* ("species circles", or here superspecies). In this matter the main thing for us is to comprehend his way of thinking and to understand his overall concept. With his assertion that morphospecies "split" into several "genera" (= subspecies) Brehm did not real-

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ly mean a "dissolution" of the morphospecies concerned but simply their taxonomic classification or subdivision. The great majority of his numerous ecological "subspecies", which each belong to a particular morphospecies and, according to Brehm, are morphologically distinguishable and replace each other geographically in (e.g.) coniferous or deciduous woodland or bushy landscapes, were "ficticious" and were not confirmed by his successors[12], but 55 of his geographical subspecies are still currently recognized (Haffer 1996, 2003, 2006).

Several 20th-century authorities believed that in his books of 1831 and 1832 Brehm had actually divided most Central European bird species into several separate species, so that, according to his ideas, in a single habitat one could see, alongside each other, a variety of species of Blackbird, Robin, Chaffinch, etc. This is a false allegation or a misunderstanding of Brehm's interpretation, because in the 1830s he *never* held such an opinion as far as the great majority of bird species were concerned. In Brehm's view at the time, in any particular habitat there mostly existed only *one* representative of a morphospecies, i.e. only one Blackbird, Robin, or Eurasian Jay. According to his view in 1831, of 311 of his subspecies of German "songbirds" (in today's sense), 289 replace each other geographically or ecologically within their respective morphospecies, while for only 22 (7%) subspecies does he claim that they live alongside another subspecies of their morphospecies in the same habitat (syntopically). However in quite a few cases his statements on distribution are very vague, so these assertions, plus a few others, should be taken *cum grano salis*.

In the course of the 1840s he became increasingly unclear in his writings about the geographical-ecological separation of a number of his subspecies, confidently asserting that in several cases different subspecies of a morphospecies occurred together in the same habitat, breeding but not hybridizing. However in many instances he himself was uncertain whether he was dealing with different taxa or with varieties (individual variations) within a population, writing: "they could be called subspecies or varieties". Then, in the 1850s, he actually interpreted most of these "subspecies" as individual variations within a single taxon, thus taking back his earlier opinion that these "subspecies" of a morphospecies represented separate sympatric taxa. Yet Brehm was not always consistent and his taxonomic views, as we have seen, altered substantially over time. This must be taken into account when considering the theoretical ideas regarding his species and "subspecies". His postulations from the 1830s on the one hand, and those mainly from the 1850s on the other, differ enormously from each other, though in both cases they are clear and comprehensible. His views in the 1840s, however, are today difficult to follow. He was dealing at length with several cases of sympatric subspecies of a morphospecies, and his writings are best regarded as "transitional" between what he believed formerly, in the 1830s, and latterly, in the 1850s. It was in this last decade that he began to adopt ternary nomenclature, giving subspecies three names (genus, species, subspecies), hence differentiating them from the binary-named species.

In his review of C.L. Brehm's ideas on avian species, Eck (2006), in tune with several authors in the 20th century, only took account of the reproductive aspect, giving attention neither to the change over time in Brehm's thinking nor to the geographical-ecological occurrence of the individual forms (subspecies) within Brehm's morphospecies. The reader might gain the false impression that all of Brehm's forms were mere fiction, yet the number of morphospecies of Central European birds distinguished by Brehm agrees almost exactly with the number of biological species.

Friderich Faber (1796–1828). The Dane Friderich (Frederik) Faber had a theoretical mind, and in his short life made many important observations on the biology and ecology of Arctic birds (Helms 1928, 1934; Stresemann 1951: 308–309). Stresemann (1928: 182) called him "one of the most innovative ornithologists" of the 19th century, who attempted to create a comparative biology of northern birds " in order to reveal the underlying causes of what is visible, and in doing so he raised himself high above his famous contemporaries like Johann Friedrich Naumann und Christian Ludwig Brehm". Faber traveled in Iceland from May 1819 until September 1821 with the intention of carrying out exact observations to obtain results that would be generally applicable. Faber, like the philosopher Immanuel Kant, was convinced that "all of Nature is nothing more than a linking together of phenomena according to laws, and there is absolutely no irregularity" (Faber 1825–1826, Foreword, p. IX). He published in Germany, initially in Oken's journal *Isis*, and belonged to the group around C.L. Brehm and J.F. Naumann, with whom he was in regular correspondence during the 1820s. In 1823 he also visited the Naumanns in Köthen and Ziebigk.

Faber had clear ideas about biological species and wrote: "Individual birds freely mating with each other in nature belong to one species" (1825: 117–118). Species can vary geographically, i.e. morphologically differentiated regional groupings (populations) do not necessarily belong to another species (as some ornithologists of the time believed, based on a strictly morphological species concept). In a letter to J.F. Naumann, Faber wrote:

"I call a bird a species when individuals freely and naturally mate and, in addition, produce young capable of reproducing themselves; it is certainly the case with *U[ria] troile* [= *Uralia aalge*, Common Murre] and *U. tr. leucophthalmus* [= 'Bridled' Common Murre] that they mate with each other but because the latter is simply a race of the former they do not lose their diagnostic features, so that

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when [they] are paired with each other the young sometimes lack a white eye ring and sometimes have one. These 2 birds resemble each other almost completely in their history and form; but this is not the case with *U. Brünnichii* [= *U. lomvia*, Thick-billed Murre] and both of the others. *Uria tr. leuc.* eggs are just like those of *U. troile* but in both of them the color of the eggs varies almost from one individual to the next" (26 March 1822; see Klein 1910).

Faber (1825–1826) distinguished between sedentary birds, non-directional dispersers, and migratory birds. The "migratory instinct" causes the last of these to depart in autumn while the "home-sickness instinct" brings them back to their breeding grounds in spring. Avian migration always takes place from the poles toward the equator, never the reverse. The further north a bird breeds the earlier it begins its autumn migration and the later it returns in spring. Male songbirds arrive in Iceland a few days earlier than females. In the breeding quarters the "home-sickness instinct" is replaced by the "mating instinct", leading to mating, nest building, egg laying, incubation, and raising the young. In monogamous birds, Faber distinguished between (a) double monogamy (both sexes raise the young together; e.g. coastal species like auks and cormorants), (b) intermediate monogamy (the young are led to the sea immediately after hatching, where they forage for food on their own; e.g. freshwater birds like *Colymbus* [= *Gavia*], *Podiceps*, *Fulica*), and (c) single monogamy (females raise the young on their own; e.g. *Cygnus*, *Anser*, *Anas*, *Mergus*). In addition, Faber talks about birds' eggs: the number in the clutch of various species, absolute and relative size (compared with the size of the bird in question), shape, surface texture, and color. Synoptic (dichotomous) tables illustrate (1) mating, breeding, and feeding situations of Icelandic birds, (2) walking ability, (3) flying ability, and (4) swimming ability of boreal waterbirds.

In his *Prodromus der isländischen Ornithologie* (1822) (Fig. 29) [*Preliminary study of Icelandic ornithology*] Faber gathered together short statements on the ecology of individual species, and in his *Beyträge zur arctischen Zoologie* (1824, 1826, 1827) [*Contributions to Arctic zoology*] he published extensive accounts – short monographs in essence – on all the birds he had observed (*Podiceps*, *Fulica*, *Phalaropus*, *Puffinus*, *Procellaria* [= *Hydrobates*], *Uria*, *Carbo*, *Colymbus* [= *Gavia*], Passeres, *Falco*, *Strix*, *Mormon* [= *Fratercula*], *Alca*). "All the qualties required to create the genuine expert were united in Faber", wrote Stresemann (1951: 308), "total command of the literature, a thorough grounding in anatomy, a sharp eye in the study of bird skins, and an understanding amounting to genius for what the biologist must look for in the field if he wishes to understand and not only describe. More critical than the enthusiastic Brehm, a finer mind than the quiet Naumann, Faber unquestionably occupies the first place in this illustrious company."

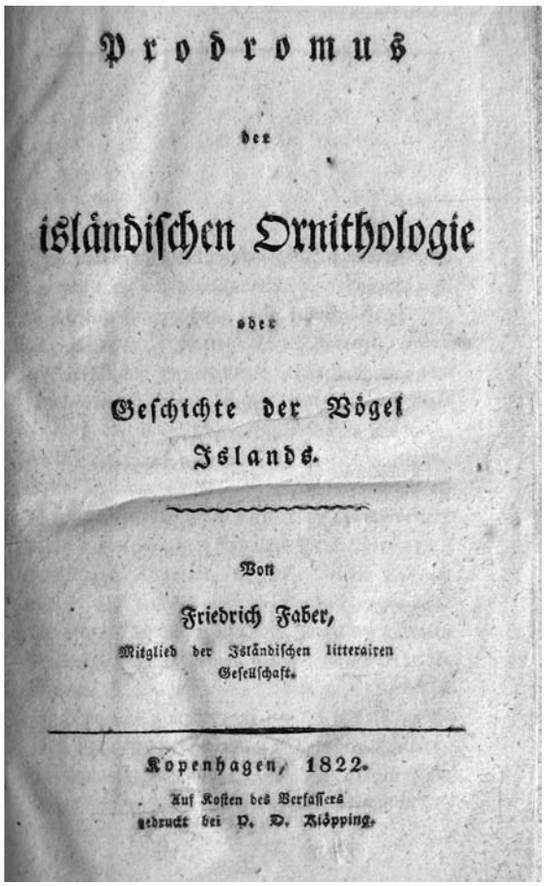
Prodromus
der
isländischen Ornithologie
oder
Geschichte der Vögel
Islands.
Von
Friedrich Faber,
Mitglied der Isländischen litterairen
Gesellschaft.
Kopenhagen, 1822.
Auf Kosten des Verfassers
gedruckt bei P. D. Klöpping.

Fig. 29. Title page of Faber (1822).

Constantin Wilhelm Lambert Gloger (1803–1863). Gloger studied the avifauna of Silesia, especially in the mountainous Riesengebirge (1827) on today's Polish/Czech Republic border (Karkonoski in Polish, Krkonoše in Czech), and published a handbook of the landbirds of Europe (1834). He had a heated dispute with C.L. Brehm about how to establish species boundaries in birds, relatively broadly or relatively narrowly (see below). But both of them had the same theoretical concept of what is generally meant by "species", namely reproductive communities (on a typological basis), a point of view widespread among German ornithologists around 1800, building on the works of the 17th-century John Ray and the 18th-century G. Buffon (e.g. Blumenbach, Zimmermann, Illiger, and Oken).

Gloger (1833: X) wrote: "Animals which mate with each other in the wild (though not only exceptionally) belong to the same species". And Brehm: "Those creatures that regularly mate with each other in a free and natural situation are of one and the same species […] No one, least of all Herr Gloger, can raise any serious objection to this definition of a species".

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So Gloger and Brehm supported the same species concept in theory, but in practice both ornithologists had very different opinions on the boundaries of the taxonomic category "species".[13] The taxonomic category of species in Gloger's system was broad and inclusive. For many species it encompassed geographical "varieties", which he described in words but did not award their own taxonomic names, given the often continuous or clinal gradients of difference between these subspecies. By contrast, C.L. Brehm's taxonomic species category was narrow, generally encompassing only a single taxonomic form or subspecies, because he assumed that subspecies of a morphospecies would not hybridize with each other. Hence Brehm was an early taxonomic "splitter", while Gloger was an early "lumper", who brought together a relatively large number of geographical forms to create very broad polymorphic species taxa. In many cases he interpreted varieties as subspecies that later would be shown to be species, such as:

Anthus pratensis (incl. *A. cervinus* and *rufogularis*)
Anthus aquaticus [= *A. petrosus* ?] (incl. *A. littoralis*)
Motacilla alba (incl. *M. lugens*)
Motacilla flava (incl. *M. melanocephala* [= *feldegg* ?])
Parus major (incl.g *P. monticolus*)
Sturnus vulgaris (incl. *S. unicolor*)
Cinclus aquaticus [= *cinclus*] (incl. *C. pallasii*)
Corvus monedula (incl. *C. dauuricus*)
Emberiza hortulana (including *E. caesia*)
Passer domesticus (incl. *P. hispaniolensis* and *italiae*)

These facts indicate that Brehm and Gloger stood for contrary and extreme positions in questions of taxonomy, yet in the final analysis both of them were mistaken. Brehm defined species too narrowly, and Gloger often too broadly. The "golden mean" that later ornithologists would arrive at on the basis of additional information lay between the extreme viewpoints of these two doyens of ornithology.

Gloger introduced some genus and subspecies names that are still valid (in **bold**)[14]:

Taoniscus Gloger, 1842 – Dwarf Tinamou
Buteo buteo ***vulpinus*** (Gloger, 1833) – "Steppe Buzzard"
Necrosyrtes Gloger, 1841 – Hooded Vulture
Tympanuchus Gloger, 1841 – prairie chickens
Bugeranus Gloger, 1842 – Wattled Crane
Neomorphus Gloger, 1827 – ground cuckoos
Bubo bubo ***sibiricus*** (Gloger, 1833) – "Siberian Eagle-Owl"
Rhinoplax Gloger, 1841 – Helmeted Hornbill
Pelargopsis Gloger, 1841 – kingfishers
Nystactes Gloger, 1827 – puffbirds
Xipholena Gloger, 1841 – cotingas
Motacilla alba ***lugens*** Gloger, 1829 – "*Trauerbachstelze*" [= *M. (a.) yarrellii* – Pied Wagtail; *M. lugens* – Black-backed Wagtail]
Terpsiphone Gloger, 1827 – paradise flycatchers

It goes without saying that Gloger – just like Brehm and the great majority of biologists prior to the appearance of Charles Darwin's epochal book in 1859 – was a typologist or essentialist, believing in the constancy (invariability) of species, and certainly not an evolutionist. To illustrate his view in this regard he quoted with great approval the contemporary botanist E. Meyer, who had written:

"The immutable integrity of species is the only fixed point around which […] their varieties revolve in continuous oscillation and dynamic, so that even an observer feels dizzy watching it in action […] Nothing is secure if the ground is not firm" (see Gloger 1833: 135).

Gloger devoted a most interesting book of lasting value to geographical variation in birds, with the title *Das Abändern der Vögel durch Einfluß des Klima's* (1833) [*The variation of birds under the influence of climate*]. Here he explained in some depth his view that "those few people who […] wish to regard climatic varieties as species must be seen as following the wrong path. What one cannot delimit one ought not to separate!" (p. 5). More than one-third of the species known to Gloger vary geographically (p. 137); he listed them in his handbook of 1834, where they are described in detail. Regarding the actual appearance of geographical variation, he noted that darker colors (black, black-brown, gray, brown, rust red) are more intensely developed in those forms of a species living in warmer climates. Conversely, in cold northern climes plumage becomes paler and whiter (pp. 12, 15). The pelt of mammals too varies with climate in the same fashion as plumage color in birds (p. 38). This phenomenon was formulated as Gloger's Rule by Rensch (1929: 152, 1934: 25), under which name it has been discussed in many major works of zoogeography and evolution (e.g. Huxley 1942: 213; Mayr 1942: 90, 1967: 256, 1984: 200, 449; Rensch 1954: 43, 47). Gloger himself (1833: 73–78) stated that "voice, song, color, and other life qualities, residence, etc., all can change", both individually in the same place or geographically. However, he did not believe that the geographical differences in the various subspecies of a particular species of bird were genetically fixed, so that if members of a form were introduced into an area occupied by another form of the same species "then after a few years they would either resemble the form native to that place, or their offspring conceived there would resemble them in the second or third generation […] climatic species cannot exist, only simple varieties" (1833: 106, 107).

Like Brehm (1827), Gloger (1829) pointed out that "the females of many open-nesting species of ducks and fowl

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are inconspicuously colored; hence Nature gives her special protection to the parent bird that is both most endangered and most important for the continuation of the species […] The color of the eggs is in many cases more or less clearly adapted to the surroundings, especially in ground-nesters like Nightingale and Sky Lark" (Stresemann 1951: 325),

Gloger popularized practical bird conservation in the 1840s (Barthelmess 1981), and when Jean Cabanis founded the *Journal für Ornithologie* in 1853, Gloger was invited to be a collaborator (see below). In the following years he published numerous commentaries and reviews on avian biology.

Professor Lichtenstein and Gloger's Rule. Gloger had grown up in the country in Upper Silesia, had attended grammar or high school in Neiße, and from autumn 1821 studied zoology in Breslau (Wrocław). Of particular importance to him was the winter semester of 1824/25, when he matriculated at the University of Berlin and for 8 months was a student of H. Lichtenstein, the professor of zoology (Möller 1972). Since the founding there of the Zoological Museum in 1810, the professor had a considerable collection of Eurasian birds and mammals at his disposal, and in his lectures and courses often drew attention to the striking geographical variations in the coloration of many species due to the influence of different climate types. This phenomenon had already been pointed out by Peter Simon Pallas (1741–1811), the great scientific explorer of Siberia and the Far East, in his important *Zoographia Rosso-Asiatica* of 1811. Lichtenstein himself published hardly anything on these important conformities, but was in full agreement with his student Gloger using the Berlin material to study geographical variation in the coloration of birds and mammals and later publishing his findings in a long paper. Lichtenstein wrote a foreword to the work, in which he stated his agreement to those elements in Gloger's thinking which he (Lichtenstein) had formulated in lectures, conversations, and letters. Following his return to Breslau in the summer of 1825, Gloger wrote a long series of letters to Lichtenstein, which are held in Berlin, although the professor's replies are missing.

A high percentage of bird species follow Gloger's Rule, whose adaptive basis is a protective or camouflage coloration to confuse predators, prey animals, or competitors. More heavily pigmented feathers and hair are also advantageous in combating damage from bacteria, which are commoner in warm humid climates than in dry ones (Burtt & Ichida 2004).

Ornithological book projects left unfinished by Gloger. In the early 1830s Gloger started several major book projects, but in each case, following publication of their first parts, abruptly abandoned and never finished them:

(1) *Vollständiges Handbuch der Naturgeschichte der Vögel Europa's, mit besonderer Rücksicht auf Deutschland* [*Complete handbook of the natural history of the birds of Europe, with special emphasis on Germany*]. Only Volume 1 (1834a) on the landbirds was published (Fig. 30). In it Gloger followed the research findings of C.L. Nitzsch, in that he distinguished between "Singing passerines. *Aves passerinae melodusae*" and "Passerines without a larynx. *Aves passerinae anomalae*". Therefore for the first time in a generalized handbook the hirundines and the swifts appeared well separated from each other. Several anonymous contemporary reviews of this excellent publication were very positive, praising the richness of the contents and looking forward to the appearance of the second volume on the waterbirds (see the journals *Reportorium der gesammten deutschen Literatur* (ed. E.G. Gersdorf), Vol. 3, 1834, p. 318; *Kritische Blätter für Forst- und Jagdwissenschaft* (ed. W. Pfeil), Vol. 9, 1835, pp. 51–54; *Isis* (ed. L. Oken), 1835, columns 413–416). Gloger summarized general aspects concerning the distribution of European landbirds in an early lecture (1832a). Volume 2, however, was never published.

(2) *Andeutungen zur zoologischen Geographie, mit besonderer Anwendung auf die Verbreitung der Vögel* [*Suggestions towards a zoological geography, with special reference to the distribution of birds*]. An announcement of this book appeared on page 2 of the prospectus and invitation to a subscription to the *Handbuch* mentioned above, issued by the book dealer August Schulz & Co. (Breslau) and dated 1st November 1833. Gloger unfortunately never finished the manuscript of this work and it was never submitted to the printers. It would have been the first global overview of the zoogeography of birds. Only the brief summary of a lecture by Gloger on the topic ever appeared (1834b). In it he states that the number of bird species and genera rapidly declines moving from the tropics to the higher latitudes, but that the area of distribution of individual species is greater in these higher latitudes than in the tropics, also that waterbirds have greater ranges than landbirds in the main, and the number of nocturnal birds increases towards the equator. Woodpeckers are absent only in the forests of New Guinea (because of "the smoothness of the bark and hardness of the wood of the native trees", according to Gloger's historically interesting ecological explanation!).

(3) *Gemeinnütziges Hand- und Hilfsbuch der Naturgeschichte* [*Practical handbook and manual of natural history*], which was intended to be a representation of the entire animal kingdom (though mostly of all mammals and birds). Once again only Volume 1 of this handbook appeared after a considerable delay: 1841 (pp. 1–400) and 1842 (pp. 401–496 and pp. I–XXXXIV). On p. III of the Foreword to this handbook

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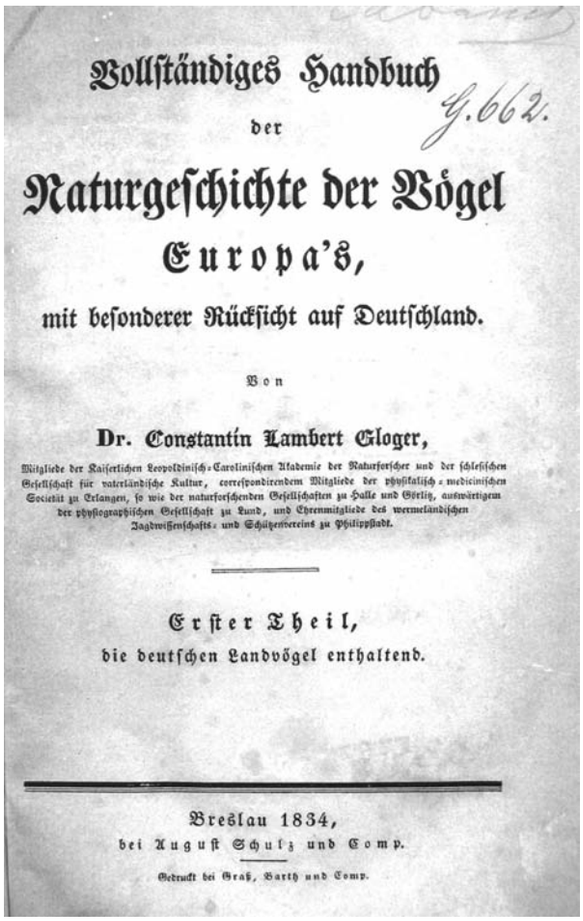

Vollständiges Handbuch
der
Naturgeschichte der Vögel
Europa's,
mit besonderer Rücksicht auf Deutschland.

Von

Dr. Constantin Lambert Gloger,

Mitgliede der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher und der schlesischen Gesellschaft für vaterländische Kultur, correspondirendem Mitgliede der physikalisch-medicinischen Societät zu Erlangen, so wie der naturforschenden Gesellschaften zu Halle und Görlitz, auswärtigem der physiographischen Gesellschaft zu Lund, und Ehrenmitgliede des wermeländischen Jagdwissenschafts- und Schützenvereins zu Philippstadt.

Erster Theil,
die deutschen Landvögel enthaltend.

Breslau 1834,
bei August Schulz und Comp.

Gedruckt bei Graß, Barth und Comp.

Fig. 30. Title page of Gloger (1834).

and manual Gloger explains that he had been unable to make headway with several ongoing projects because of an eye ailment, but has been able to dictate this particular manuscript without carrying out further research. Even if various health problems in the 1830s had interfered with his work, it remains difficult to understand why he didn't turn to the completion of these three unfinished books later in life. What was the reason for this strange behavior?

Our study of unpublished material in the *Geheimes Staatsarchiv* [State Archives] in Berlin has shown that after the beginning of 1834 Gloger's scientific endeavors were suddenly diverted towards a completely different subject, which from then on would command his full attention (Haffer & Hudde 2007). It was for this reason that he abandoned the projects outlined above. From then on his energies were dedicated to his work on what he called *Gloger's Natürliches System der Thierwelt* [*Gloger's natural system of the animal kingdom*], a theoretical construction built on natural philosophy which he imagined as the high point of his intellectual life and career. This was now his life's work, for which, at the age of only 30, he was to sacrifice his extremely promising ornithological future, as we must confirm in retrospect.

Grammar school teacher in Breslau. In July 1830, the same year in which he gained his PhD, Gloger was appointed to the position of natural history teacher at the Matthias Gymnasium in Breslau. However he regarded the job only as a transitional occupation until he would be able to take up a post as university lecturer or professor of zoology. This apparently became so obvious to his superiors that a few years later they recorded that Gloger "is not suited for this school and can in no way be commended in the conscientious undertaking of his teaching duties or in his official diligence. He gives nothing in return for his remuneration" and shows a "complacent evaluation and self-conceited notion of his own worth" (Provincial School Board of Breslau, 9 August and 14 October 1836; personal file on Gloger, *Staatsarchiv*). Again and again during the 1830s Gloger wrote petitions for the financial support of his scientific research and applied unsuccessfully for the position of associate university professor. These documents can still be studied in the Berlin State Archives, in the file on Gloger from the "Royal Ministry of Spiritual, Educational, and Medical Affairs". In September 1842, when the minister concerned, Dr. Eichhorn, pressured by Gloger's insistence, finally approved a 3-year stipend of 600 Reichsthaler per year "towards the furthering of his project", Gloger happily left his permanent, yet detested post at the Breslau grammar school on 31 December 1842. He immediately moved to Berlin as a private scholar "in order to be able to devote all my time and energy to the service of science in a place with access to the required literature" (Gloger on 25 March 1861; Rep. 87 B, No. 19998, Sheet 287; *Staatsarchiv*). This "service" referred to the long-promised elaboration of "Gloger's Natural System of the Animal Kingdom".

Natural philosophy as the supposed highpoint of Gloger's life and work; the role of Professors Steffens and Nees von Esenbeck as Gloger's teachers. Between ca. 1800 and 1840 many German biologists were influenced in their thinking by the Romantic *Zeitgeist* and by the idealistic natural philosophy of Friedrich Wilhelm Schelling and Lorenz Oken. They taught the unity of nature and the human mind, believing that what was required was "to show the genesis of the world out of the human mind […] An entirely new perception of Nature must arise, based on Idealism" (Kühn 1948: 216). They believed that deductive knowledge of nature was possible and that the genesis of the animal world may be understood through theoretical thinking without laboriously assembling an inductive basis of observed facts. When the scientific untenability of such notions was later recognized there was

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much complaining about "the pointless waste of great energies and valuable time" and "Schelling's corrupting influence" on the biology of the day in such works as *Ideen zur Philosophie der Natur* (1797) [*Ideas towards a philosophy of nature*] or *System des transzendentalen Idealismus* (1800) [*System of transcendental idealism*].

As pointed out above, since the early 1830s Gloger too had fallen under the influence of this biological *Zeitgeist*, having clearly been "seduced" by the teachings of his professors at the University of Breslau, above all Henrich Steffens (1773–1845) and C.G.D. Nees von Esenbeck (1776–1858), both prominent representatives of the natural philosophy school in Germany. The former taught in Breslau between 1811 and 1832, when he was called to Berlin. He saw Man as a living unity of mind and nature, and one of his published works dealt with the main principles of "philosophical science", a glorification of Schelling's worldview (Liebe, in Hennicke 1893). "Because of Steffens' almost paternal affection for me from the very beginning, I have been completely indebted to him," Gloger wrote on 3 April 1830 to Profesor Lichtenstein in Berlin, and again on 26 September of the same year: "Prof. Steffens, who shows the interest of a father in me and who does everything in his power for me". Also in 1830, Steffens contacted the Minister of State with a recommendation for financial support for Gloger, saying that he saw in him "a most excellent future teacher of natural history" (*Staatsarchiv*).

The well-known natural philosopher Nees von Esenbeck also taught at Breslau University from 1830 to 1851. "He has always been meticulous, more meticulous than anyone else, has known about my project from the very start [= 1834] and has most attentively followed its progress", wrote Gloger (Letter 1 to the Crown Prince in 1838; *Staatsarchiv*). The natural philosophy of his professors' lectures and writings had heavily influenced Gloger's thinking since the early 1830s.

Work on Gloger's Natural System of the Animal Kingdom. On 7 January 1834, the 30-year-old Gloger believed that he had been granted "an enlightened inspiration by Providence[15] concerning the discovery of the system underlying all of nature", which he regarded as the "hoped-for turning point for the better" in his life. He immediately started on a new undertaking, "which consists of a large-scale zoological systematics and will contain the unexpectedly rich results of a happy idea in a moment of illumination" (letters 1 and 3 to Crown Prince Friedrich Wilhelm in 1839[16]).

Gloger felt that he had been found worthy of "a discovery far more influential than any granted to previous naturalists". Providence had chosen him "to achieve for the first time not only the most difficult task but one that had been thought to be almost impossible!". He felt himself to be "a weak tool for such an important task, though one chosen by a higher power and equipped at least with the best of intentions". Ultimately he saw in his system a "proof of the necessity of the existence of God" (letter 3 to the Crown Prince).

In his applications for support to the Prussian Academy of Sciences in Berlin in October/November 1835 and January 1838, Gloger explained the principles of his systematics, which he said would have to be in agreement with "simple empiricism as well as a refined natural philosophy" (*Staatsarchiv*).

The position of individual animals or forms in the system, either "lower" or "higher", is always determined by "one and the same numerical principle". All forms occupy a definite and unalterable position, and in this the use of particularly problematical taxa is essential, since their position makes that of neighboring taxa evident. The systematic arrangement never follows a simple line but instead is constructed of ever smaller parts of largely parallel and analogous lines of forms of equal number, and this is true for genera as well as species and varieties, and hence an arrangement in the form of tables is best suited for depicting the natural system.

In addition, from a step-wise arranged natural system, Gloger was hoping to find the underlying formative rules (*ursprüngliche Bildungsgesetze*). The natural system and the history of nature would then be perfectly congruent and be as one.

According to the explanations in his letter to the Crown Prince of 11 December 1838, this natural classification "will have to develop into a calculation with forms (here organic structures) similar to the role played by algebra in connection with mathematics, a calculating and constructing in quantities and forms. It has in common with those two that a majority of forms and factors needs to be known in order to allow the calculation and deduction of those entities that are still unknown".

Following his "enlightened inspiration" of January 1834, whose exact nature he never revealed, as early as 29 March of that year Gloger presented the Ministry of Spiritual, Educational, and Medical Affairs with a tabular overview of the vertebrates and of the entire animal kingdom based on his "new method". Lichtenstein received a letter on 18 June 1836 accompanied by special tables on the system of mammals, listing essential genera, while on 6 July the Prussian minister von Altenstein was sent five tables of the mammals glued together plus a universal table of the entire "world system", which can be inspected today in the Department of Ornithology of the Berlin Museum of Natural History. For a detailed account see Glaubrecht & Haffer (2010), which forms the basis of much of the remainder of this chapter.

Gloger's *Universal Table of the World-System* divides *Seyn* [*Being* or *Existence*] into *Schöpfer (Ursache)* [*Creator (Cause)*] and *Welt (Wirkung)* [*Cosmos (Effect)*]; the

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latter consists of (a) systems of fixed stars and galaxies/nebulae and (b) planets with no life and planets with life, i.e. the Earth. The zoological tables carry the general title *Gloger's Natural System of the Animal Kingdom*. The mammals for example are divided into *non-walking (flying and swimming)* and *walking (terrestrial) mammals*. The first group includes those with *wing membranes* (i.e. bats) and *flipper feet* (seals, whales, etc.). The terrestrial mammals are classed as *higher terrestrial mammals* and *lower terrestrial mammals*, distinguished from each other by (e.g) complete or incomplete rows of teeth, presence or absence of hooves, and similar morphological criteria. A detailed main table contains "mammals down to all genera". These tables are similar to dichotomous identification keys, but fail to make the huge significance given to them by Gloger clear to a modern observer. But above all it is impossible to discern how he actually utilized his "natural philosophical numerical principle" to arrive at this classification.

Other natural philosophers at this time also predicted the existence of undiscovered genera or species on the basis of certain "numerical principles", such as 4 or 5 genera per family or species per genus (Stresemann 1951: 184–185). But Gloger's "calculation with forms", his predictions, and systematic categorization of unknown taxa are not closely explained and his method cannot be gleaned from the study of his tables. The only concrete example in the substantial bundle of letters and manuscripts surviving is the family of "toothed" pangolins, whose existence Gloger said he had "worked out" using his system before their discovery (letter to Lichtenstein of 14 February 1838).

These unpublished explanations of his system by Gloger himself, only briefly summarized here, are marked by much pathos, immense long-windedness, and few comprehensible facts. Hence his requests for financial support were often met with skepticism and reservations. On 18 August 1842 the Prussian Academy of Sciences wrote to the minister responsible about Gloger's plan to work on the systematics of vertebrates, pointing out that his idea was based on the personal error that the apparent success of his treatment of a small part of the mammals permitted him to be optimistic and to immediately expand his research to the entire animal kingdom. Herr Gloger ought to rather employ his excellent observational talent, "which has enabled him to gain outstanding knowledge in the area of the higher animals, in specialized studies, namely the completion of his natural history of European birds". To the Academy it appeared "dubious to vouch in advance for the alleged success of his enterprise, which after all only aims at a formal framework" (*Staatsarchiv*). The zoologists of the Academy, among them C.G. Ehrenberg in particular, had seen through the emptiness of Gloger's project on natural philosophy.

Gloger apparently continued to work on his ambitious plans for a system encompassing the whole of the animal world until at least 1850, since in that year he wrote to J.F. Naumann, informing him that he was still occupied with his "natural system" and so would be doing no further work on the second volume of his European handbook (Möller 1972: 57–58). The increasing criticism of natural philosophy throughout Germany in the 1850s probably made his situation ever more difficult, so that Gloger finally abandoned his dream of a "Natural System of the Animal Kingdom".

Work on pest control and animal conservation. Gloger's theoretical studies based on natural philosophy produced no concrete results, and at the end of 1845 his stipend was exhausted. When the Ministry refused any further payments he was forced to think of some way of providing an income for himself, and started to write papers on pest control and the protection of economically useful animals to sell to the Ministry of Agriculture, which did indeed provide him with small and irregular payments for a certain length of time. He then turned to writing on bee-keeping and the cultivation of hemp, on game protection and agriculture, and to papers on damage caused by vermin, especially voles and mice, the conservation of birds, in particular hole-nesters, and other useful animals (Haffer & Hudde 2007).

In doing this Gloger acted in the interest of the balance of nature and for the conservation and protection of all animals useful for this balance, so he was one of the founders of an advanced ecological form of animal conservation (Barthelmess 1981). His suggestions of how to combat pests through artificially increasing the numbers of their natural enemies were based on ideas of Professor Lichtenstein, who, in his unpublished *Bemerkungen zu den Berichten und Gutachten über die Feldmäuse am Rhein im Jahre 1822* [*Remarks on the articles and reports about the voles on the Rhine in the year 1822*] (1823) had written:

"Without doubt the natural methods, i.e. those most immediately supplied by nature, are best […] They consist primarily in the deliberate encouragement of an increase in numbers of the natural enemies of the voles." It ought therefore to be "deprecated in the extreme to shoot a Sparrowhawk, Goshawk, Buzzard, Kestrel, or owl. […] An increase in polecats, martens, and weasels would do a great deal towards the eradication of the voles. They should be caught in an organized fashion and released in the fields where the voles are doing damage" (Rep 87 B, No. 19998, pp. 27–30; Staatsarchiv)

The response in Germany to Gloger's popularly written articles in daily newspapers and in agricultural and forestry publications was divided, though abroad it was more

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Fig. 31. Portrait of Constantin W.L. Gloger in 1862 with the Order of St. Stanislaus (from Glaubrecht & Haffer 2010; Museum für Naturkunde Berlin, Historische Bild- und Schriftgutsammlungen).

friendly. In 1862 the Russian Czar even awarded Gloger the St. Stanislaus Order 3rd Class for his work on pest control (Fig. 31).

Return to ornithology: biology of birds. When Professor Jean Cabanis, ornithologist at the Museum of Natural History in Berlin, founded the *Journal für Ornithologie* in 1852 (the first issue appeared in 1853) he invited Gloger to be a collaborator, doubtless paying him a small fee for his help and for his numerous contributions (a total of 128 after all!) to this new journal during the last ten years of his life. He wrote on some of his observations in Silesia decades earlier as well as on various aspects of avian biology in general, stimulated by his study of the ornithological literature. He apparently lacked the money even to undertake excursions or make field observations in the surroundings of Berlin.

Among the subjects he dealt with in the first year of the *Journal* were the acrobatic climbing ability of Little Bittern in its reedbed habitat, Northern Pintails swimming just below the water surface, or hybridization between duck species. In the following year (1854) there were articles on various aspects of the reproduction of the Common Cuckoo, the hybridization of Western Capercaillie and Black Grouse, the attraction of shiny objects for some birds (which Gloger thought could be connected to their diet, e.g. metallically iridescent beetles), plus remarks on the food of Great Spotted Woodpecker and gulls dropping hard-shelled mollusks on rocky ground (1855). In an interesting note he drew attention to the fact that (according to Nilsson) young curlews can already hear, recognize, and respond to the calls of their parents while they are still in the egg (1856), and later in the same year he wrote about family bonds in birds and the supplementary molt in the Red Grouse *Lagopus l. scotica* in Scotland. In later years he discussed bird migration across the sea (1857) and "cock nests" in birds (1859). Gloger explained the greater length of wing and tail feathers in immature Golden and White-tailed Eagles by their need for more effective flight feathers than the adults because they move around so much, while older birds become increasingly sedentary (1860); for further details see Haffer & Hudde (2007).

But the small incomes he received for his contributions to the *Journal für Ornithologie* and his papers for the Ministry were eventually insufficient to cover even the most basic necessities. Ratzeburg (1868: 201, footnote; 1874: 81, footnote) rather unfairly described Gloger during that decade as "having gone astray", and of living "idly" or "indolently". Gloger attended at least two *Deutsche Ornithologen-Gesellschaft* conferences, 1851 in Berlin (where he was even reconciled with his old adversary C.L. Brehm, thanks to J.F. Naumann acting as go-between) and 1856 in Köthen (where he delivered a verbose lecture on the definition of species, though the conference was unable to agree on the taxonomic limits of the species taxon), but otherwise lived a very secluded life as a lonely private scholar and bachelor, having failed in his three-decade long attempt to classify nature. (Möller 1972: 82) related his sad end: "He lodges with Widow Schulze in Berlin [-Charlottenburg], Mauerstr. 80, and she, along with her son, sometimes has to support him." Finally his poverty was compounded by sickness and Gloger died on 30 December 1863 of "abdominal dropsy".

C.W.L. Gloger's approach to species – even if he regarded them as reproductive communities – was essentially typological and he delimited many bird species in polytypic fashion, which was quite in contrast to other ornithologists of his time. In what we would call today "lumping", he subsumed many of the geographically variable climatic varieties (subspecies) of birds within one species, hence he argued against taxonomic names for subspecies. This caused later authorities, for example Stresemann (1951: 72), to judge Gloger's view as having led systematic ornithology into a dead end, whereas we propose that his approach stimulated fruitful and ultimately helpful discussions on species taxa and concepts and on the practical question of how to delimit species. Both the synthesis of similarities as well as the analysis of geographical differences between populations are necessary and lead to fresh knowledge in ornithology. The historical significance of Gloger's early ornithological work is now being generally acknowledged (Haffer 1992, 1997b, 2001, 2006; Haf-

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fer & Hudde 2007). In his later life his tragic struggle with classification holds both a message and a warning. Highlighting the danger of fatal error and complete failure, his *Natural System of the Animal Kingdom* stands as one of the many alternative classification schemes and attempts of the 19th century, representing systematists' continuous endeavor to bring order into the seemingly chaotic assemblage of animal taxa. For a more detailed account, including illustrations of Gloger's system and tables, see Glaubrecht & Haffer (2010).

(7.) Ornithology of the late 19th and early 20th centuries

(7a.) Faunistics and life histories of birds

Bird collections and natural history museums. Bird collections in museums form the basis for systematic and zoogeographical studies, for research on individual and geographic variation, studies of plumage color patterns, biodiversity and other topics. Public and private bird collections were very important during the period when ornithology originated as a separate branch of science. Ornithologists of the early 19th century who owned bird collections were, among others, Count Hoffmannsegg near Dresden, Bernhard Meyer in Offenbach, and Christian Ludwig Brehm in Renthendorf (Thüringen).

When the University of Berlin was founded in 1810, Count Hoffmannsegg presented his collections of birds and insects to the new Museum of Zoology (under Carl Illiger and later M.H.C. Lichtenstein) as a foundation on which to build in future years. Similary, Bernhard Meyer's collection formed the basis of the Senckenberg Museum in Frankfurt a.M. under P.J. Cretzschmar. In 1825, four other public centers existed besides those mentioned above: Darmstadt (under J.J. Kaup), Munich (under J.B. Spix and J. Wagler), Dresden (under L. Reichenbach), and Halle (under C.L. Nitzsch). These and other museum collections in Germany grew steadily during the 19th and 20th centuries, especially after Germany had established colonies in Africa, New Guinea, and the Pacific Ocean during the early 1880s. These colonies were lost with the outcome of the First World War. In 1916, the Senckenberg Museum was able to purchase Count von Berlepsch's collection (built up from 1860 to 1910) comprising 55 000 specimens, the largest private bird collection ever assembled in Germany. Other private collections were those of O. Kleinschmidt (now in the museums of Bonn and Dresden), V. von Tschusi zu Schmidthoffen (now in the Vienna museum), and the old collections of Prince Maximilian zu Wied-Neuwied (purchased by the American Museum of Natural History, New York; a total of 4000 specimens), and of C.L. Brehm (now in the museums of New York and Bonn; the original total was 9000 specimens). Scientists and commercial collectors from central Europe traveled widely overseas, contributing to the growth of the regional knowledge of the avifaunas of the world (Stresemann 1975; Mearns & Mearns 1998; Hinkelmann 2000). See Fig. 32.

As listed by Mearns & Mearns (1998), the German collections among the important museum collections in Central Europe today are of the order of 60 000 bird specimens (Munich, Stuttgart), 75 000 (Bonn, Dresden), or 90 000 (Frankfurt a. M.). Only the collections in the Museums of Natural History in Vienna and Berlin reached totals of 100 000 and 140 000 bird specimens respectively. Additional museum collections are those in Braunschweig (30 000), Hamburg (30 000), Basle (26 000), Bremen (20 000), Halberstadt (Museum Heineanum, 18 000), Köthen (Naumann Museum), Halle, and Bern. Besides the bird collection of the Zoological Museum of the University of Hamburg, an important private "South Sea Museum" of the wealthy merchant J.C. Godeffroy existed in the city from 1861 until 1885. It was founded to augment the knowledge of ethnology and zoology of Oceania. G. Hartlaub and O. Finsch described (often in the *Journal des Museums Godeffroy* 1871–1879) the many ornithological novelties which professional collectors and the captains of Godeffroy's merchantmen sent home. After the company experienced economic difficulties this museum was closed and the valuable collections were auctioned off in 1885 and scattered all over the world (Stresemann 1975: 229). The following publications deal with the history of the main bird collections in Germany mentioned above: Munich (Hellmayr 1928; Reichholf 1992), Bonn (Rheinwald & van den Elzen 1984), Dresden (A.B. Meyer 1897), Frankfurt a.M. (Naumberg 1931; Steinbacher 1967), Berlin (Stresemann 1922; Ahrens 1925; Mauersberger 1994a), Braunschweig (Blasius 1897; Boettger 1954; Hajmassy 1983), Bremen (Duncker 1953), Halberstadt (Quaisser & Nicolai 2006; Nicolai et al. 2009), and Halle (Taschenberg 1894; Piechocki 1971). See also (e.g.) Rheinwald (2003), Roselaar (2003), and Steinheimer (2006). The sizes of these museum collections are modest compared to the collections of the British Museum in Tring or of the American Museum of Natural History in New York, each of which contains about 1 million specimens. However the old European collections are very important scientifically because they contain the type specimens on which many species and subspecies of birds are based. Besides the "skin" collections which preserve the skin and plumage, bill and feet of a bird, museums have also built up collections of skeletons and of birds preserved in alcohol serving as research material for anatomical and functional-morphological studies.

Oology. The collection and study of avian eggs was quite fashionable among private collectors in Europe during the 19th century, and a large series of well-illustrated books

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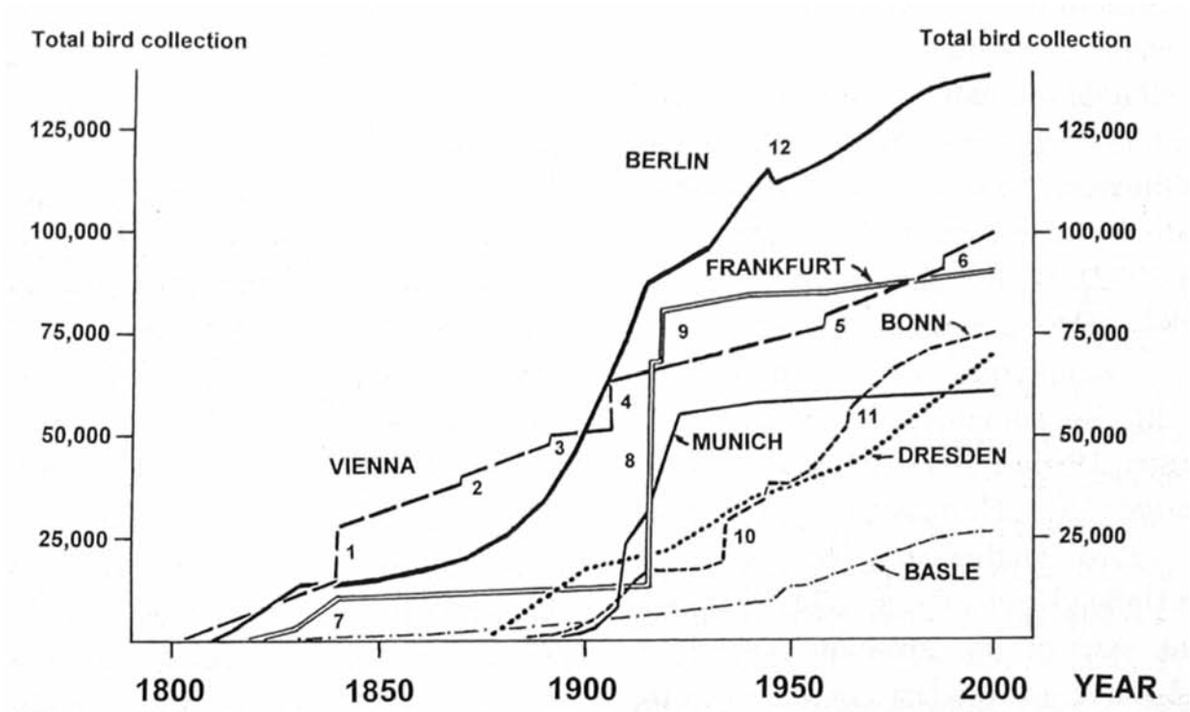

Fig. 32. Growth of the bird collections of some museums in Central Europe. Numbers indicate major collections incorporated into the respective museums: 1 – Natterer; 2 – "Novara"; 3 – Reischek; 4 – Tschusi and Grauer; 5 – Schiebel; 6 – Seilern; 7 – Rüppell; 8 – Berlepsch; 9 – Erlanger; 10 – Kleinschmidt; 11 – C.L. Brehm; 12 – indicates losses during and immediately after the end of the Second World War (from Haffer 2001, which see for sources).

on the subject has been published (Zorn 1742, 1743; Klein 1766; Günther 1772; Naumann & Buhle 1818–1828; Schinz 1819–1830; Thienemann et al. 1825–1838; Thienemann 1845–1856; Morris 1853–1856; Baedecker et al. 1855–1867; des Murs 1860; Graessner 1860, 1880; Wolley & Newton 1864–1907; Reichenau 1880; Oates & Hume 1889; Poynting 1895–1896; Seebohm 1896; Nehrkorn 1899; Rey 1899–1905; Oates & Ogilvie-Grant 1901–1912; Dresser 1905–1910; Krause 1905–1913; Jourdain 1906–1909; Pelt Lechner 1910–1914; Koenig 1931–1932; Kobayashi & Ishizawa 1932–1940; Hellebrekers 1949; Hoogerwerf 1949; Matousek 1956; Schönwetter 1960–1992; Verheyen 1967; Makatsch 1974, 1976; Cramp et al. 1977–1994; Mikhailov 1997). Schönwetter's 4-volume *Handbuch der Oologie* (1960–1992) is more satisfactory than previously published ones. This, however, does not make him the "founder of scientific oology", as Piechocki (1999) stated in his title without any justification to substantiate his claim. The founders are rather among the oologists of the mid-18th century listed above (Nitze 2000).

The *Journal für Ornithologie* regularly carried scientific notes and articles on (e.g.) the individual and geographical variations in egg color in particular species, the characteristics of the egg of the brood-parasitic Common Cuckoo (relatively small size, strong shell, similarity in color to the host's eggs), differences in the structure of the eggshell in closely related species, the eggs of bird species from overseas and other topics. Blasius (1861) discussed at a *DO-G* meeting the question whether or not birds' eggs have species-specific characteristics. The first discussions of the significance of measurements and weights of eggs were those of Reichenow (1870) and Nathusius (1882). The latter's studies on the structure of eggshells in different groups of birds were combined and republished in an English translation almost a century later (Tyler 1964). An oological journal, *Zeitschrift für Oologie und Ornithologie*, appeared from 1891 to 1924 (volumes 1–29). Some oologists published heated discussions in the *Journal für Ornithologie* (1877–1879) about the applicability of Darwin's theories, especially his proposed mechanism of natural selection, to the evolution of the color and shape of birds' eggs (F. Kutter for and W. von Nathusius against; see also Kutter 1889 and Hartert 1890). Some of the current uses of extant egg collections are display, research, and identification as discussed by Walters (1994). Rahn et al. (1985a, b; 1988a, b; 1989a, b) analyzed and evaluated Schönwetter's data from various oological and physiological viewpoints. The gradual thinning of eggshells of several common European species during the last few decades due to environmental influences (DDT) was documented on the basis of historical egg collections (Green 1998).

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Behavioral observations. Another controversy among Central European ornithologists from the late 1860s onward was sparked by the evolutionary and anthropomorphic views of animal behavior as expressed by Alfred Edmund Brehm (1829–1884, the son of Christian Ludwig Brehm, in his popular books on *Das Leben der Vögel* (1861, 1867) [*The life of birds*], *Thiere des Waldes, Wirbelthiere* (1864) [*Forest animals, vertebrates*], *Illustriertes Thierleben, Vögel* (1866–1867) [*Illustrated animal life, birds*], and *Brehms Thierleben, Vögel* (1876–1879) [*Brehm's animal life, birds*]. His adversary was the zoology professor Bernard Altum (1824–1900), who countered Brehm's interpretation in his book on *Der Vogel und sein Leben* (1868) [*The bird and its life*]. Both ornithologists made excellent observations on bird behavior but differed profoundly in their interpretations. Natural-theological (Altum) and anthropomorphic views (Brehm) were both held by many scientists in Europe from the 18th into the 19th centuries without major disputes. It was the great popularity of Brehm's *Animal Life* which provoked Altum into writing his teleological and anti-Darwinian book, leading to a vigorous public debate. Brehm himself (1868, 1876: 20–24), A. & K. Müller (1868, 1890), and K. Ruß (1868) attacked Altum, the latter answering these criticisms in later editions of his book. The discussions on *Instinct and deliberate actions of higher animals* by A. & K. Müller (1869: 8–16) indicates that their views were less extreme than appears from their highly emotional book review (1868). They, in fact, did accept the existence of instinctive behavior in animals that has remained constant for "an unimaginable time" and stated that "instinct as a cogent law dominates the entire animal world". They went one step beyond Altum when they claimed that "instincts are peculiar not only to the animal's soul but even man acts at times instinctively". However, they continued, at least higher animals also act to a higher or lesser degree deliberately. The animal's free self-determination proves the indubitable relationship of its soul with that of man (see also A. & K. Müller 1890: 69–81).

A.E. Brehm, who adhered to a Darwinian view of evolution, was a great popularizer of the study of animal life. The two main aspects of his work were (1) his emphasis on the habits of animals and (2) his anthropomorphic interpretation of animal behavior. In his writings Brehm frequently cited his own observations of birds, also those of his father C.L. Brehm and of J.F. Naumann among German ornithologists, as well as the writings of naturalist travelers overseas like Heuglin, Audubon, Radde, Gould, Burmeister, Wallace, Azara, Darwin and many others. He combined his personal expedition experience in northeastern Africa, Spain, Norway and later in Siberia with that of many other adventurers, writing brilliantly and enthusiastically about animals as living beings in their environments in a style accessible to the general public. His publisher distributed Brehm's book in several languages and in large editions worldwide.

Brehm's anthropomorphic interpretation of animal behavior was derived from the romantic natural philosophical views prevailing among many European zoologists of the first half of the 19th century (e.g. C.L. Brehm, L. Oken, J.F. Naumann, P. Scheitlin; see Stresemann 1975: 319, Jahn & Wolf 1979, and especially Schulze 2009). According to Brehm, in their actions animals reveal "sympathy", "compassion", "love", "hatred", "gratitude", "vanity", "sense of honor", "pride", etc. He disliked the predominantly analytical academic zoology. The nature of the ornithological accomplishments of father and son Brehm during the first and second halves of the 19th century were totally different from each other, and a direct comparison of their writings, their significance and influence, as attempted by some authors (e.g. Dathe 1989), would seem impossible. Brehm senior was a researcher and systematist who addressed a relatively small group of colleagues. As mentioned above, he also published many functional observations on birds (Stresemann 1975: 302), discussions of their plumages and color changes, and he discovered the specific distinctness of the members of several pairs of sibling species among the birds of Europe: (*Galerida theklae/G. cristata, Parus salicarius/P. palustris [= Poecile montana/Poecile palustris], Regulus ignicapilla/R. regulus, Certhia brachydactyla/C. familiaris*). Although the names of *G. theklae* and *R. ignicapillus* were introduced into the literature by his son A.E. Brehm (1857) and his colleague J.C. Temminck (1820) respectively, the specific distinctness of these two species had been established by the elder Brehm. This is clear in the case of the *Regulus* species (where Temminck referred to the manuscript of C.L. Brehm), but less so in the crested larks. Indirect evidence is provided by the labels of the type specimens of *G. theklae* which J.H. examined at the American Museum of Natural History (New York). These birds had been identified by A.E. Brehm in his pencil handwriting as "*G. undata*" (= *G. cristata*); C.L.Brehm crossed out his name on the labels and wrote in his characteristic handwriting with black ink "*Theklae*". With respect to ornithology as a science, Christian Ludwig Brehm's fame far exceeds that of his son, even though the latter's books have been read by many more people than those of his father.

In his book *Der Vogel und sein Leben* (11th edition 1937) Bernard Altrum opposed Darwinism and A.E. Brehm's – and many other authors'– anthropomorphic views of animal behavior (Kraus 1914). As a natural theologian he defended a teleological interpretation of a balanced harmony of creation but, with respect to the behavior of animals, he had the merit of reintroducing into ornithology the concept of instinct and innate behavior patterns. Altum insisted that when a bird is singing it does not express its feelings and has no conscious intention. "The animal does not think, does not reflect, does not es-

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tablish aims for itself and if it nevertheless behaves purposively, then someone else must have thought for it" (*Animal non agit, sed agitur*, "an animal does not act, but is acted upon", or more freely "An animal does not act by its own volition, but reacts to stimuli [drives]"; Mayr 1935). Altum thought that birds are no machines (as his opponents understood him as saying) but living organisms capable of adapting to local conditions to a certain degree. We emphasize that Altum's rejections of Darwinism did not affect his praiseworthy battle against Brehm's anthropomorphism. Altum discovered territory in the life of birds and its adaptive meaning. His ecological studies on the food of raptors and owls as well as his discussions of the "economic value" of birds were other important contributions at a time when the bird protection movement was gathering momentum.

We know today: "Alfred Edmund Brehm rightly stated that, in their emotions, higher animals may be very similar to humans. However, it was not consistent to base on this similarity his view that the behavior of animals can be guided by reason and morals, and even better so than in humans. By contrast, Bernard Altum perceived correctly that the species-specific instinctive behavior patterns of birds occur blindly and without any understanding of their functions. But he did not realize that in humans this is also partly true and followed Descartes's opinion of animals being soulless machines. … Many an exasperated conflict of opinion has been unmasked, through Charles Darwin's insights, as a spurious dispute. Today, total unanimity prevails among scientists about his theories" (Lorenz 1974: XIV; see also 1973: 10). Lorenz also stated that "Birds are much more stupid than people believe; however, in their feelings and passions birds differ much less from humans than many people presume". Lucanus (1911, 1925, 1926) and Bölsche (1924) commented similarly on the debate between Brehm and Altum stating that both were right to some degree, but wrong in many respects; as so often in life the "golden mean" appeared to Lucanus the correct approach.

The work and publications of Brehm and Altum represent the first highlight of behavioral observations of birds in Europe (besides the pioneering work of Pernau and Zorn that we have already covered). However, neither a science of animal psychology nor the idea of experimental field studies existed during their lifetimes. Moreover, most scientific ornithologists of the late 19th century were of the opinion that studies of birds in the field were only "second class" and do not contribute important biological data, thereby indirectly discouraging such work, as expressed for instance in the following well-known quote:

"Popular ornithology is the more entertaining, with its savor of the wildwood, green fields, the riverside and seashore, bird songs and the many fascinating things connected with out-of-door-Nature. But systematic ornithology, being a component part of biology – the science of life – is more instructive and therefore more important" (Ridgway 1901:1–2).

Even though Altum's book of 1868 was read very widely during those years, and six editions had appeared before 1900 (five additional ones were issued up to 1937), none of the Central European ornithologists of the late 19th century picked up his suggestions regarding the instinctive behavior of birds and began to study, describe, and analyze birds' activities in detail. German ornithology concentrated instead on the study of local fauna, avian phenology, and old-fashioned biology. Publications like J. Rennies's book on nest building, *Bird-architecture* (1844; a German translation entitled *Die Baukunst der Vögel* appeared in 1847), had no influence. In this booklet the author deviated from the usual systematic treatment and classified birds on the basis of their differing manners of nest construction (digging, platform-building, braiding, weaving, stitching, cementing, etc.). Concluding, the author stated that the instinct which guides the birds is not blind but is closely related to reason, if not really the same talent. However the abilities of animals always remain the same, whereas those of mankind progress during the course of time.

Bird migration continued to be explained by "inherited habits" until Gätke (1891) eventually concluded that migrants act on the basis of instincts, as the teleologists, including Altum (1868), had maintained long before (Stresemann 1975: 325, 333, 345). The detailed study of instinctive behavior in birds commenced in Germany, when Valentin Haecker discussed bird song in 1900 and Oskar Heinroth spoke about his researches on the behavior of the Anatidae at the Fifth International Ornithological Congress in Berlin in 1910. In Britain, a new generation of field ornithologists (e.g. E. Selous, F. Kirkman, and E. Howard) emphasized the need for detailed observations of birds' habits and behavior from around 1901 (Stresemann 1975: 342–344; see also the section on the "David Lack and the New Avian Biology" below).

Increasing emphasis on ecology, behavior, quantification of occurrence, and species richness: 1900–1999. Many ornithologists at the turn of the 20th century believed that most or all that can be known about European birds had already been discovered and compiled, especially in Naumann's classic handbook (1820–1860). This misconception led to the publication of a slightly revised edition of this work in 12 folio volumes between 1897 and 1905. Actually the available ornithological knowledge at that time represented no more than the first foundations of study, and served only to outline in a general way the life histories of the more common bird species in the region. The literature of the late 19th century usually fails with regard to the biological details of nest life, ecology, and social behavior patterns. One man opened a breach in the walls erected by the Naumann cult, as Stresemann

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(1975: 345) put it, and he was Oskar Heinroth (1871–1945), who had pointed out certain shortcomings in Naumann's work (Heinroth 1917, 1930). He was interested in the details of life history and habits of birds, i.e. things not found in Naumann's and Brehm's publications.

The large handbooks on or including the birds of Central Europe published during the 20th century are those of Hartert (1903–1922, three volumes and one supplementary volume with F. Steinbacher, 1932–1938) with an emphasis on systematics, Niethammer (1937–1942, three volumes) and Glutz von Blotzheim & Bauer (1966–1997, 14 volumes). They are characterized by an increasing emphasis on quantifying the occurrence of bird species in different areas and documenting ecological and behavioral patterns of each species based on the rich literature that had become available. The 14 volumes of the *Handbuch der Vögel Mitteleuropas* summarize the entire knowledge of Central European birds in a highly organized manner and truly represent a "New Naumann" for the 20th century, influencing the preparation of the nine-volume British handbook edited by Cramp et al. (1977–1994) as well as that of other handbooks published in neighboring countries (e.g. Romania and Czechoslovakia); see Schulze-Hagen (2013). Chapters on the grouse, partridges, and allies have been translated into French and widely used in fieldwork on these birds in the French Alps.

The handbooks have been supplemented by numerous other works on the avifaunas of Germany, Austria, and Switzerland as well as of many individual German states (e.g. Krohn 1925; Kuhk 1939; Tischler 1941; Heyder 1952; Klafs & Stübs (1979, 1987); Rutschke (1983, 1987); Knorre et al. (1986); Hölzinger et al. (1987–). We list here a selection of important titles in chronological order: Fatio et al. (1889–1956); Kleinschmidt (1905–1937, 1913, 1934); Goeldi (1914); Schnurre (1921); Friderich (1902–1904, 1923); Heinroth & Heinroth (1924–1933); Groebbels (1938); Noll (1941–1942); Bauer & Rokitansky (1951); Corti (1952); Berndt & Meise (1959–1966); Stresemann, Portenko et al. (1960–2000ff); Glutz von Blotzheim (1962); Rokitansky (1964); Wüst (1970); Wolters (1975–1982); Schifferli et al. (1980); Bezzel (1982); Dvorak et al. (1993); Winkler (1999); Bauer & Berthold (1996); Eck (1996); Schmid et al. (1998); Bauer et al. (2005). Summaries of quantitative mapping efforts in most European countries have been edited by Hagemeijer & Blair (1997). Bezzel (1982) discussed the composition of the Central European avifauna, its occurrence in the cultural landscape, its long-term dynamics, species richness, and population densities and their variation on test plots of different size, while Bairlein (1996) summarized the research results into the physiological ecology and synecology of European birds. Other disciplines that developed during the 20th century are ecomorphology (e.g. Bock 1977, 1994; Leisler 1977), ethology, the study of orientation behavior in migratory birds, and population biology (discussed in some detail below). Brief reviews of ornithological work after the Second World War with an emphasis on the political separation of East and West Germany are those of Neumann (1995) and Rutschke (1998).

General prehistorical and historical aspects of birdlife in Central Europe are an increase in diversity due to the settlement of large areas by humans, and the ensuing alteration of closed woodland into highly structured mosaic landscapes several centuries ago (Bezzel 1982; Berthold 1990a; Gatter 2000). Declines in the populations of birds and a reduction in diversity began during the first half of the 19th century caused by direct persecution and habitat destruction, leading to a period of accelerated decline due to almost complete ecosystem destruction by humans into the 20th and 21st centuries. Global warming in the future will certainly have a severe effect on the composition of the Central European avifauna (see e.g. Bairlein 2011; Sybertz & Reich 2011; Wormworth & Şekercioğlu 2011). Some predictions may possibly be formulated on the basis of the results that will be obtained through a study of the effects of the "Little Ice Age" of the 16th century and other climatic changes on the European bird fauna (Kinzelbach 1995c).

(7b.) Avian systematics

Microsystematics and speciation. During the 19th century, the specialists in the museums of London, Leiden, Paris and Berlin by necessity worked with relatively few specimens from far-distant collecting stations. Most of them described any morphologically different bird as a different species, sometimes even male and female of one species. The widespread occurrence of geographical variation within species was unknown or little known to these workers, most of whom applied a narrow morphospecies concept, (e.g.) G.R. Gray, R.B. Sharpe, P.L. Sclater in Britain, C.J. Temminck in the Netherlands, L.P. Vieillot and R.P. Lesson in France, J. Cabanis and A. Reichenow in Germany. Intermediate specimens between such "species" were regarded as hybrids possessing no more significance than any other abnormal animal. These museum ornithologists greatly increased our knowledge of the regional diversity of the avifaunas of the world but none of them pondered seriously the problem of distinguishing real species from local varieties. This was done clearly and in great detail on the basis of long personal experience and extensive bird collecting by several European explorer-naturalists who, during the late 18th and the first half of the 19th centuries, traveled in Russia, Siberia, and the Far East, men such as Pallas, von Middendorff, Eversmann, von Schrenck, Radde, or Seebohm.

Hardly any of these explorer-naturalists had a museum affiliation in Europe. They published the results of their studies privately in costly expedition reports with limit-

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ed distributions. Therefore their consistent emphasis on broadly defined polytypic species entities of Eurasian bird and mammal species, together with their impressive database on geographical variation, did not have the impact among fellow workers that would have been desirable. Even though the explorer-naturalists found some support from Gloger (1833) and Schlegel (1844), the museum specialists' view on narrowly defined morphospecies in their influential publications continued to dominate systematic ornithology, and the work of the explorer-naturalists fell into oblivion. Eventually, however, their taxonomic views prevailed decades later, mainly through the influence of the explorer-naturalists of North America (e.g. Audubon, Nuttall), via museum men like Baird, Coues, Allen, and Ridgway.

Essentialistic (typological) views dominated systematic ornithology in Europe during the 19th century, irrespective of whether taxonomists applied narrow (Linnaeus "school") or wide species limits (Pallas-Schlegel "school"; see Fig. 33).

It was assumed that a Platonic "type" (essence) underlay each species; these were conceived as immutable natural entities which had independent origins (Mayr 1982; Haffer 1997a,b). The replacement of these "schools" by modern Darwinian views through the work of the Seebohm-Hartert school beginning in the 1890s caused considerable friction. This is obvious from the contrast between Hartert and most of his ornithological colleagues in Britain, as well as between Stresemann (1889–1972) and Kleinschmidt (1870–1954) in Germany. No such difficulties developed in North America, where the evolutionary Baird-Coues school replaced, but did not overlap with, the earlier essentialistic Wilson school.

Johann Heinrich Blasius (1809–1870), Professor of Zoology in Braunschweig, was one of the spokesmen for German ornithology during the 1860s. Like most of his colleagues he was a creationist and taught that an unshakeable order rules organic nature, as it also rules the worlds of crystals and stars. Animal species were assumed to be rigidly delimited and to represent proof of an eternal order from the beginning of the world; no species ever gave rise to a new species. Hermann Schlegel in Leiden was convinced, like C.L. Brehm and the entomologist Schaum in Germany, as well as Agassiz in North America, that all geographical varieties had also existed since the beginning of creation and were immutable (Stresemann 1975). Blasius and Bernard Altum (1824–1900) emphatically opposed Darwin's theories when the young Gustav Jaeger (1832–1917) dared to discuss these new views at the annual meeting of the *Deutsche Ornithologen-Gesellschaft* in Stuttgart (September 1860). Like Blasius, Altum and Otto Kleinschmidt (1926) also propagated essentialistic (typological) views. However they had no followers and the Pallas-Schlegel school ceased to exist when Kleinschmidt died in 1954 (Haffer 1997b).

Because Kleinschmidt delimited species taxa widely, he joined forces with the early members of the Darwinian Seebohm-Hartert school in their struggle against the Linnaeus school around 1900. Its early members were Hartert himself, Schalow, A.B Meyer, Hellmayr and, a few years later, Stresemann (Seebohm had died in 1895). They applied trinomial nomenclature, designating subspecies of polytypic species with a third name, as proposed by Schlegel (1844) and the ornithologists of the North American Baird-Coues school. Others declined the use of subspecies names, despite the fact that they applied similarly wide taxonomic species limits. They recommended (as F. Faber and C. Gloger had done earlier in the 19th century) describing in words the geographical variation of widespread species without the application of formal subspecies names, because they believed that "subspecies" are merely "climatic varieties" with no genetic basis. On the other hand, some workers of the Linnaeus school did not deny the existence of geographical varieties of species in nature, yet they assigned binominal names to these subspecies as C.L. Brehm had done decades earlier (Haffer 1992: 120, 1996); for example J. Cabanis of the Zoological Museum in Berlin who published on "*Merops mentalis* nov. subsp." (*J. Ornithol*. 37 [1889]: 76). It is clear that the meaning of binomial names as applied during the 19th century varied appreciably between different systematists. Zoologists accepted trinominal nomenclature for subspecies only from the early 20th century onward.

History of the biological species concept. Many ornithologists and other naturalists of the 19th century applied a biological species concept based on the interbreeding of conspecific individuals and reproductive isolation between the representatives of different species; Gloger, for instance, stated in 1833 that "What under natural conditions regularly pairs, always belongs to one species". By stressing "regularly" he wanted to eliminate complications due to occasional hybridization. Henry Seebohm in Britain was the first ornithologist to emphasize geographical isolation as the *conditio sine qua non* for speciation to occur, and he came close to a biological species concept when he wrote that during geographical isolation two forms may "become so far separated that, should their areas of distribution again overlap they will nevertheless not interbreed, and the two species may be considered to be completely separated" (1881: X). See also Wagner (1889).

The entomologist Eimer (1889:16) said "Species are groups of individuals which are so modified that successful interbreeding with individuals of other such groups is no longer possible" (similarly Standfuss 1896: 336, 353). Two British entomologists, Karl Jordan (born and educated in Germany) and Edward Poulton, discussed the nature of biological species in great detail in several articles published in 1896, 1903, and 1905 (see Mayr 1982). Their work was in the tradition of Darwin's concepts of grad-

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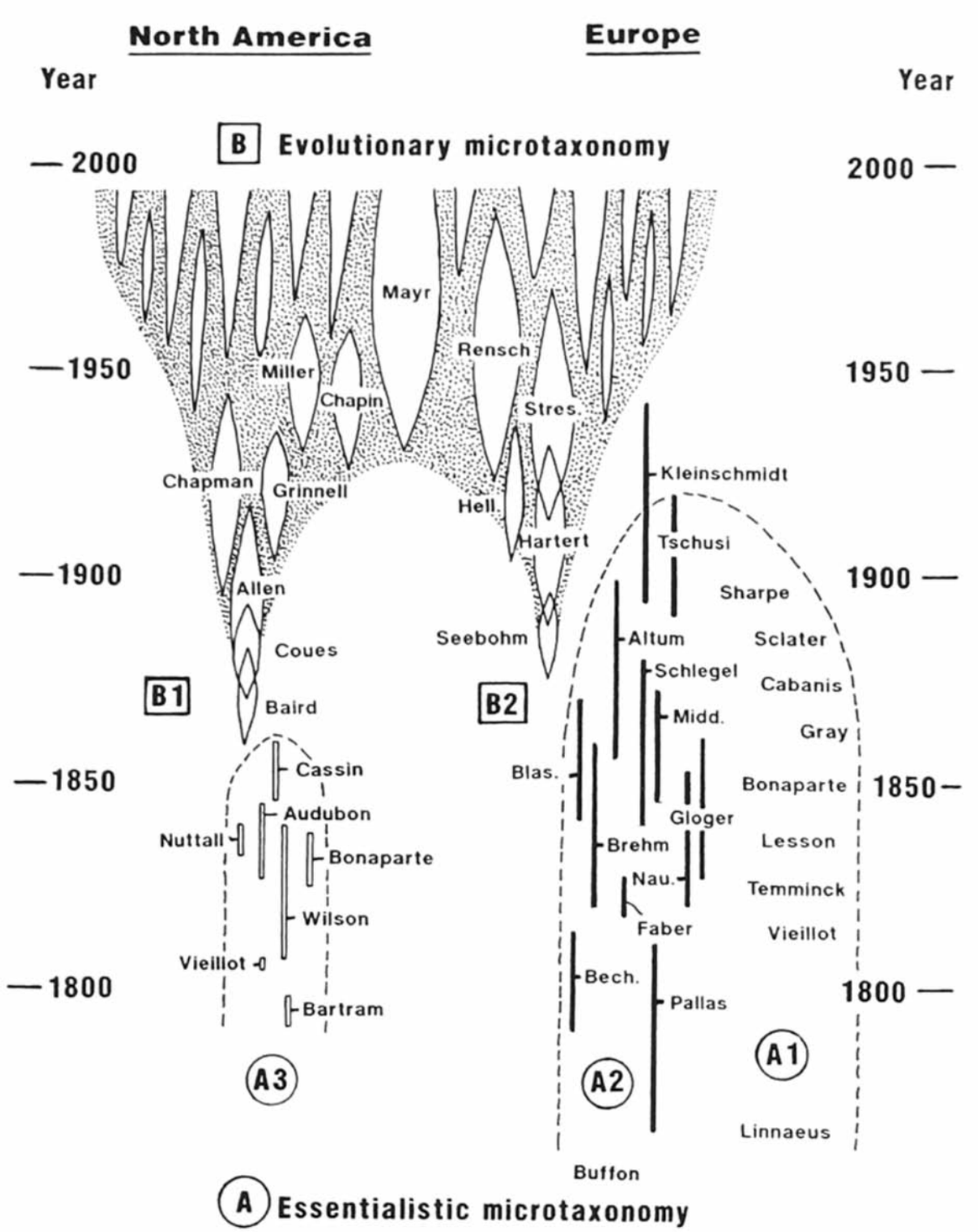

Fig. 33. Research traditions ("schools") of systematic ornithology during the 19th and 20th centuries. A. Typological (essentialistic) microtaxonomy; A1. Linnaeus school, A2. Pallas-Schlegel school, A3. Wilson school; B. Evolutionary microtaxonomy; B1. Baird-Coues school, B2. Seebohm-Hartert school. The main publishing periods of major ornithologists are indicated symbolically. Most presently active representatives of evolutionary microtaxonomy are indicated anonymously. Bech. – Bechstein, Blas. – J.H. Blasius, Midd. – Middeldorff, Nau. – Naumann, Stres. – Stresemann. (From Haffer 1997a).

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ual evolution and speciation through the differentiation of populations in geographical isolation (allopatric speciation). Ludwig Doederlein (1902) emphasized that – as long as we remain at a particular time level (in the case of fossils or extant animals) – species are sharply delimited from one another and produce no fertile hybrids. He also discussed in detail geographical variations in relation to the mobility of the species concerned.

Since pre-Darwinian times ornithologists had recognized the need to collect "series" of specimens of a species from individual localities, i.e. more or less extensive population samples, to understand individual and geographical variation. Thus by 1900 the populational analysis of species was routine for students of mammals, birds, fishes, snails and some other groups (Mayr 1980:127). Ernst Hartert who – under the influence of Seebohm, the North American ornithologists, and later K. Jordan – delimited species taxa broadly, published a list of the biological species of birds inhabiting the Palearctic Region (1903–1922). L. Plate (1914) conceived the species "physiologically", stating that a species comprises all individuals which reproduce together sexually; a common bond between them facilitates mutual recognition and sexual reproduction. As early as 1919, Stresemann also adopted a biological species concept: "Forms which have reached the species level have diverged physiologically to the extent that, as proven in nature, they can come together again without interbreeding. Morphological divergence is independent of physiological divergence" (1919: 64, 66). In the case of allopatric taxa, their taxonomic rank as subspecies or species is to be determined by inference based upon several auxiliary criteria. In several articles he interpreted the increased variability of certain populations of Central European birds as due to secondary contact and hybridization of the parent populations involved. Stresemann criticized the recognition of formally named subspecies in continuously (clinally) varying populations of birds. During the 1920s his investigations of polymorphic species (where he labeled the morphs as "mutations") linked ornithology with genetics. He treated species as aggregates of populations which often vary clinally and discussed population phenomena, such as the population continuum zones of secondary intergradation and geographical isolates. Through this work, Stresemann (followed by B. Rensch and E. Mayr) introduced the methodology of the "New Systematics" into ornithology during the 1920s and 1930s, and it was these ornithologists who made the decisive contributions to the development of the biological species concept and the problems of speciation (Mayr 1982; Haffer 1992). From 1913 onward, Stresemann routinely applied the theory of allopatric speciation, i.e. the origin of species from small and geographically isolated populations. He was the first to develop a model of speciation for European subspecies and species of birds from populations isolated in Mediterranean refugia during glacial periods in the Pleistocene (Haffer et al. 2000). Krementsov (1994: 36–41) completely neglected the contribution of Central and western European zoologists to the development of the New Systematics and the biological species concept when he compared the work of Russian and "western" (i.e. North American) biologists of the early 20th century. His discussions are totally inadequate, particularly where he claims that many of these achievements originated with the publications of Russian entomologists at that time.

The discovery of geographically representative forms which do not or only rarely hybridize along their zones of contact, and for this reason represent biological species (Rensch 1928, 1929), eventually led to a reversal of the excessive taxonomic "lumping" tendency among ornithologists, which had reached a peak in Europe under the influence of Kleinschmidt's (1926) views. Kleinschmidt delimited very broad *Formenkreise* ("species circles" = polytypic species), which often included as subspecies geographically representative species. The publications of Rensch (1929, 1934) and later Mayr (1942) were the first comprehensive statements of population systematics in Europe.

Comparable to the events in North America, an "Evolutionary Synthesis" between the experimental-reductionist tradition of the geneticists and the observational-holistic naturalists (biological systematists and paleontologists) also occurred in Germany between 1937 and 1950 (Junker & Engels 1999; Junker 2000; Reif et al. 2000). A crucial contribution toward the "synthetic" programs of those years was the close cooperation between Stresemann and the population geneticist N.W. Timoféeff-Ressovsky (1900–1981) in Berlin during the period 1940–1945 (Haffer 1994a, 1999). They discussed the genetic basis of geographical variation and genetic effects during range expansion in various bird species. Following a lecture by Stresemann (1943) on the species concept and on the implications for the speciation process of ecological differences in subspecies and species (see Stresemann 1943), Timoféeff-Ressovsky (1943) emphasized how fruitful the cooperation had been between the more theoretically oriented genetic-evolutionary teams and the systematists and zoogeographers during recent years, leading to full agreement regarding the nature of the evolutionary mechanisms. A joint study by Stresemann & Timoféeff-Ressovsky (1947) on speciation in birds was completed in 1944 but not published until after the end of the Second World War. Timoféeff-Ressovsky's arrest by the Soviet authorities in 1945 prevented further studies in this series that were planned.

Examples of ornithologists in Central Europe who conducted studies of birds on the basis of the New Systematics and within the framework of the Seebohm-Hartert school during the second half of the 20th century are W. Meise, G. Niethammer, and G. Diesselhorst (birds of

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varoius regions of the world), J. Martens, S. Eck, A. Helbig, M. Kaiser, and A. Gebauer (Palearctic birds), H. Schifter and R. van den Elzen (African birds), J. Haffer, C. König, and K.-L. Schuchmann (Neotropical birds). Many of these studies included the application of modern methods of morphological and vocal analyses as well as molecular DNA analyses.

Several alternative notions of the general nature of species (theoretical species concepts) conceive these units as created entities (typological concept), as groups of non-intergrading populations at any particular time level (biological concept), or as phyletic lineages through geological time (phyletic and evolutionary concepts). These theoretical concepts need to be distinguished from the different (wide to narrow) taxonomic delimitation of individual species taxa (Table 1). Under each of these theoretical species concepts biologists have delimited and are delimiting "narrow" and "wide" species taxa (splitters and lumpers respectively) depending on whether these systematists place the taxonomic species limit at relatively "low" or "high" levels of microtaxonomic differentiation respectively. A species limit at a fairly high level of differentiation results in relatively few species taxa, each species comprising wide arrays of variously differentiated geographical representatives. On the other hand, a taxonomic species limit at a low level of differentiation results in more numerous, internally rather uniform and narrowly defined species taxa. Zoologists advocating different theoretical species concepts might in practice delimit species taxa in a similar manner. Those, on the other hand, adhering to the same theoretical species concept might delimit species taxa quite differently.

Problems regarding the nature of species in animals generally, and the delimitation of species taxa in particular, have again been the subject of extensive discussion in the recent literature (Haffer 1992, 1997c; Helbig 2000). In a few cases, detailed work has indicated that the members of closely related European birds can no longer be considered as representing subspecies of one biological species (as has been the case for a long time) but are species just beyond the level of species differentiation (e.g. *Oenanthe hispanica/O. pleschanka* and *Phylloscopus collybita/Ph. brehmii*). However, it is important to realize that, in these cases, both the earlier and modern taxonomic interpretations refer to the same species limit under the biological species concept. On the other hand, the limit of "phylogenetic species" is placed at a much lower level of differentiation. Even taxa intergrading along broad zones of hybridization (subspecies under the biospecies concept) are considered as binomially named "species" under the phylogenetic species concept.

Zoogeography. The methods of a static 19th century zoogeography led to the subdivision of the world into numerous faunal regions and subregions of animal distribution based on faunal lists and their greater or lesser resemblance (e.g. Reichenow 1888; Schalow 1897). Beginning during the 1910s, Erwin Stresemann viewed zoogeographical problems within ornithology from a dynamic-ecological point of view. His method of zoogeographical analysis stressed the need to examine the dispersal abilities and distributional ranges of individual species, as well as the ecological and geological history of particular regions to understand the zoogeographical history and differentiation

	Species concepts				
Species limits	**Typological**	**Evolutionary**		**Historical**	
		morphological	biological	cladistic	paleontological
Wide	Gloger 1833, 1834 Middendorff 1850s Kleinschmidt 1920s	Geyr 1924 Meinertzhagen 1954 Eck 1985	Hellmayr 1920s Stresemann 1919–1927		
Intermediate	Brehm 1831 Schlegel 1844 Blasius 1862 Dubois 1871	Allen 1870s Baird 1870s Coues 1870s Ridgway 1870s Dwight 1918, 1925	Seebohm 1880s Hartert 1903–1922 Stresemann 1928 ff. Rensch 1929, 1934 Mayr 1942, 1963 Lack 1944, 1947 Bock 1979, 1986	Hennig 1966 and followers Willmann 1985	Simpson 1961 and other paleontologists
Narrow	Temminck 1815 Vieillot 1816 Hartlaub 1877 Sclater 1880s Sharpe 1899–1909	Berlepsch 1911 Reichenow 1913	Stepanyan 1974, 1978	Cracraft 1983 Zink 1996, 1997	

Table 1. Theoretical species concepts (horizontal) and species limits under different taxonomic species categories (vertical) as applied by some ornithologists during the 19th and 20th centuries. Years refer to major publications; slightly altered after Haffer (1992).

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of a genus or family of animals as a dynamic and continuing process. Based on this method he analyzed the zoogeography of selected groups of European and Afrotropical birds in a series of papers published between 1919 and 1929 (e.g. Stresemann & Grote 1929), while F. Steinbacher (1927, 1929) studied how the distributional ranges of selected European bird species resulted from historical processes. Stresemann returned to this subject in a more comprehensive manner in his analysis of the avifauna of the Malay Archipelago that forms the introduction to his monograph *Die Vögel von Celebes* (1939) [*The birds of Sulawesi*]. In this magnificent work he emphasized the need to take into consideration the possibility of active range expansion of island birds across ocean barriers, and of montane birds across lowland gaps, without the need to postulate the former existence of land bridges or mountain bridges, as had been done by many previous zoogeographers. He concluded that – apart from sea-level changes – several very humid and dry climatic periods had alternated during the Pleistocene, leading to drastic changes in the distribution of forest and non-forest vegetation and corresponding faunal movements and differentiation.

Stresemann's dynamic-zoogeographical interpretations of faunal movements and speciation in tropical Africa (1929, with Grote) and the Malay Archipelago (1939) were pioneering contributions during those years. The basic premises of his theories of speciation based on climatic-vegetational fluctuations have been amply confirmed during later decades for the Palearctic Region (de Lattin 1967), Australia (Keast 1961), tropical Africa (Moreau 1966), and South America (Müller 1973; Haffer 1974).

Comparative anatomy. The comparative study of the anatomy of animals is one of the oldest zoological research traditions, pursued with the aim of establishing a natural system and of understanding the functioning and biological roles of particular structures and organs. Blumenbach (1779) had emphasized that the animal's entire *habitus* needed to be taken into consideration when judging its systematic relations, and Blasius Merrem (1788: 4) also asserted that "The similarities of all parts of the body taken together, not of individual parts, must determine genera, tribes, orders, and classes" (cited from Stresemann 1975: 107). These positions were again defended by Carl Illiger (1811) and B. Merrem (1813). In this latter work the large ratites were placed in a group separate from all other birds because they lacked a keel on the sternum. Friedrich Tiedemann (1810, 1814) summarized the then available anatomical knowledge in a thoroughly researched handbook published in two volumes. Christian Ludwig Nitzsch (1782–1837), "outstanding both for his minutely detailed research and for his acute reasoning" was "one of the most accurate, cautious, and imaginative morphologists who ever concerned themselves with avian anatomy" (Stresemann 1975: 236, 308). He published *Osteografische Beiträge zur Naturgeschichte der Vögel* (1811) [*Osteological contributions to the natural history of birds*], a monograph on the nasal gland (1820; see also Giebel 1858), and observations on the carotid artery in birds (1829). In this latter study, he aligned the swifts with the hummingbirds, moving them a long way from the swallows. Nitzsch studied each bird that he received from a pterylographic (study of feather tracts) and anatomical point of view, and searched its plumage and intestines for parasites which he also investigated from various viewpoints. He contributed detailed chapters on the anatomy of the genera of European birds treated in J.F. Naumann's great *Naturgeschichte*. After Nitzsch died in 1837, Rudolph Wagner (1805–1864) in Munich continued these contributions for the last volumes. Wagner had published a major treatise on the anatomy of birds in 1837. Several of Nitzsch's manuscripts were edited and published by his colleagues after his death (e.g. Nitzsch 1840; Giebel 1858, 1862, 1866). Keyserling & Blasius (1839) announced that they had discovered a useful character of the songbirds (except the larks Alaudidae): their "booted" tarsometatarsus.

Another outstanding zoologist who devoted his attention, at least temporarily (during the 1840s), to the anatomical study of birds was Johannes Müller (1801–1858), who established the major divisions of the Passeriformes (1847) based upon characters of the syrinx, separating the New World (Tyrannidae) and the Old World flycatchers (Muscicapidae). Later descriptive studies of the syrinx were those of L. Wunderlich (1884), V. Haecker (1900), and his student W. Köditz (1925).

Max Fürbringer (1888) and Hans Gadow (1891, 1893) had the great merit of augmenting the knowledge of the anatomy of birds in an unsurpassed manner when they published in large volumes the results of their painstaking studies over many years. Their classifications are the basis of most or all later natural systems of the birds proposed during the 20th century. Gadow was interested in the comparative anatomy and taxonomic relevance of the avian digestive system, an interest which much later led Ziswiler (1967; Ziswiler & Farner 1972) to study the anatomy of the digestive system and the systematic position of granivorous songbirds. Leiber's (1907) detailed work on the tongue of the woodpeckers may also be mentioned here.

Following the publication of Fürbringer's and Gadow's volumes, interest in comparative anatomy with a systematic and phylogenetic perspective faded away and only a few studies appeared in Germany (e.g. Krause 1901, Martin 1904) until modern evolutionary morphology flourished again through the work of D. Starck (born in 1908) and his students (Barnikol, Fiedler, Hofer, Lang) in Frankfurt a. M. from the mid-20th century (Duncker & Fischer 1999). They studied the morphology of the head (Hofer 1955) and the jaw muscles supplied by the trigeminus

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nerve, concluding that the falcons are more closely related to the owls than to the other groups of diurnal raptors (Starck 1959). The Amazonian Hoatzin (*Opisthocomus hoazin*) occupies a very isolated taxonomic position because of the occurrence of many primitive characters which, during the course of evolution, have been transformed in other birds through various specializations (Barnikol 1953). The above authors also assembled evidence to suggest that the Apteryges (Apterygidae and Dinornithidae) are widely separated from the other ratites. Glutz von Blotzheim (1958) believed that the carinate birds and the ratites evolved separately from different groups of coerulosaurs.

Macrosystematics and evolution. In his *Prodromus* (1811), Carl Illiger (1775–1813) rejected the old-fashioned beak-foot classification of Linnaeus and followed the position of his intellectual precursors J.F. Blumenbach and B. Merrem. He recognized for birds 7 orders, 41 families, and 147 genera. During the early and mid-19th century, many German scientists were influenced by the natural philosophy of F.W.J. Schelling and Lorenz Oken. In his *Natürliches System der Vögel* [*Natural system of birds*], L. Reichenbach (1852) divided each category level into *four* subdivisions, whereas J.J. Kaup based his *Classifikation der Säugethiere und Vögel* (1844) [*Classification of mammals and birds*] on the "sacred number five". For a British example of this "quinarian system" see MacLeay (1819–21, 1825), which was carried into ornithology by W. Swainson (1836). After 1859, even evolutionists like A.E. Brehm and Reichenow defended practical systems that facilitated quick identification. Brehm (1866–1867) used the categories of crackers (parrots, finches, and corvids), catchers, searchers, runners, and swimmers, similar to the classifications of 16th-century authors. The anti-evolutionist E. von Homeyer also grouped birds following an outdated system (Stresemann 1975: 239). Other prominent anti-Darwinians were (e.g) Schlegel, Altum, and Blasius.

Morphological systematics: In his classic volumes *Untersuchungen zur Morphologie und Systematik der Vögel* (1888) [*Studies on the morphology and systematics of birds*] Max Fürbringer (1846–1920) kept in mind the connections between form and function as well as the allometric growth of parts. Hans Gadow's system of birds in Bronn's *Classen und Ordnungen* [*Classes and orders*] is similar and the Fürbringer-Gadow system became the basis of the current classification of birds, the Wetmore-Peters system (Bock 1990a). Because of the uncertainties of classification fixation at high taxonomic levels, Stresemann concluded: "In view of the continuing absence of trustworthy information on the relationship of the highest categories of birds to each other, it becomes strictly a matter of convention how to group them into orders. Science ends where comparative morphology, comparative physiology, comparative ethology have failed us after nearly 200 years. The rest is silence" (1959: 227–228). However the subsequent developments in molecular science outlined below show that he was being too pessimistic!

His intention was to emphasize that the classic methods of comparative studies will not fill the considerable gaps in our understanding of the relationships of many higher-level taxonomic groups (orders) of birds. In the meantime biochemical methods of analysis have been applied to this problem with varied success (egg-white proteins, blood proteins, lipids in the uropygial gland, sequencing of mtDNA and nuclear DNA; Sibley & Ahlquist 1990). Bock (1992) is optimistic that progress in macrosystematics will be achieved on the basis of functional-adaptational investigations of taxonomic characters. He illustrated this approach with the results of several studies, (e.g.) the monophylogeny of all paleognathous birds including the tinamous, the isolated taxonomic position of the passerine finches, the non-homology of the foot structure in galbulids and picids, and the isolated position of the Hoatzin (*Opisthocomus hoazin*), often wrongly held to be a cuckoo.

The results of several other attempts to solve macrosystematic problems are here briefly summarized:

Oological systematics: Few avian orders as currently recognized are corroborated by the characters of the egg shell, although detailed comparisons are still lacking. On the other hand, oological characters support the delimitation of many suborders, families, subfamilies, and genera. In many cases, oology supports the separation of certain taxa; for instance the eggs of *Opisthocomus* differ conspicuously from those of cuckoos, and the eggs of sandgrouse (Pteroclidae) differ from those of the pigeons and doves (Columbidae). In many other cases, oological characters argue against the lumping of genera or recommend their splitting. Many other "contradictions" may be understood as adaptations to breeding in cavities, in open sites, in colonies, or as a consequence of a change to brood parasitism (Meise 1976; see also Kutter 1889, Hartert 1890, and the long series of oological textbooks published during the 19th and 20th centuries outlined above).

Plumage and feather change (molt): Nitzsch (1840) analyzed the pterylography of most major groups of birds and found similarities between (e.g.) hornbills and hoopoes, gulls and shorebirds, pigeons and sandgrouse, nightjars and owls, as well as swifts and hummingbirds. He was one of the first to note pterylographic differences between the four groups of raptors (diurnal raptors, Old World vultures, New World vultures, owls), he separated the barn owls (Tytonidae) from the typical owls, and found that passerines usually have ten primaries but that the outermost is always shorter than the others and is absent in some species. Many groups of non-passeriform birds lack the fifth secondary feather in the wing (diastataxis or

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aquintocubitalism) (Gadow 1893). Steiner (1918, 1956) and Stephan (1970) studied this phenomenon, which the latter interpreted functionally; the diastataxic gap developed several times independently in different groups when the wing had to be folded more tightly as a result of evolutionary changes in proportions (e.g. a relative lengthening of the humerus, of the lower arm bones, a relative shortening of the femur, and other reasons).

From a macrosystematic viewpoint, the study of molt patterns in birds turned out to be rather disappointing. No single mode of replacement of flight feathers is common to two orders of birds (Stresemann & Stresemann 1966). However certain peculiarities of the molt of primaries (P) characterize a number of families: the falcons (Falconidae) begin with P4 from where the molt proceeds in both directions, outwardly and inwardly, whereas the hawks (Accipitridae) change their primaries in a normal descending order. Cuckoos (Cuculidae) have a transilient mode, while many parrots (Psittacidae) follow Hampe's Rule, beginning with P6 from where molting continues outwardly and inwardly. Each of the three subfamilies of the kingfishers (Alcedinidae) has its own particular molt sequence. Two more recent publications treating the plumages and molt of European birds are those of Bub (1981–1988) and Jenni & Winkler (1994).

Modern ornithology during the 20th century

During the 19th century and until about 1920 ornithology and general zoology were widely separated. Few ornithologists in Central Europe and other areas of the world were interested in the research of anatomists, physiologists, geneticists, and psychologists. Conversely, general zoologists worldwide viewed ornithology as the *scientia ambilis* of amateurs, the results of whose work could not mean much to researchers in the field of wider zoology. During the 1920s, however, ornithology rapidly changed and general biological studies were emphasized over the earlier systematic-faunistic work. It was soon recognized that the bird is particularly well suited for studies into the basic problems of speciation, functional morphology, physiology, behavior, and orientation of animals. Ornithology became an indispensable part of modern biology. This transformation of ornithology as an occupation for taxonomic and faunistic specialists into a branch of modern biological science during the 1920s and 1930s was largely led by one man: Erwin Stresemann (1889–1972). During those years he was Secretary of the German Ornithologists' [formerly Ornithological] Society (*Deutsche Ornithologen-Gesellschaft*, *DO-G* formerly *Deutsche Ornithologische Gesellschaft*, *DOG*) (Haffer 1994a, 1997a, 2007a,b; Haffer et al. 2000). This accomplishment was of greater general significance and had broader consequences than his important ideas on species, speciation and zoogeography of birds. We emphasize that the "Stresemann revolution" in ornithology was not restricted to Central Europe but had a worldwide impact. It was at that time that ornithology became part of biology, indeed assumed a leading role in the discipline. For this reason Ernst Mayr (1997b: 855) stated: "I think one can say truthfully that no one in the last 100 years has had as profound an impact on world ornithology as Erwin Stresemann". When he had just "thrown the switch", so to speak, and was beginning to work on the new program for ornithology, Stresemann said: "Our task will be to work on ornithology giving up its previous isolation and achieving a respected position within the system of scientific zoology. . . . A wide field of activity lies ahead of us and thereby the prospect of a bright future for our science" (Stresemann 1926a: 231). This revolutionary vision led to Stresemann's farsighted support of exciting new research areas like functional morphology, behavior, and orientation of birds, as well as of promising young scientists like B. Rensch, E. Mayr, K. Lorenz, G. Kramer and others (see Fig. 33).

(8.) The Stresemann Era

Erwin Stresemann as an innovator

Career. Stresemann accomplished the transformation of ornithology into a New Biological Ornithology (or New Avian Biology) by adding avian physiology, functional morphology, ecology and behavior to the narrower older ornithology when he (a) published his masterpiece, the outstanding volume *Aves* (1927–1934) in the *Handbuch der Zoologie* [*Handbook of Zoology*], (b) skillfully edited two ornithological journals from 1922, (c) supervised a large series of PhD dissertations, and (d) encouraged a number of other major ornithological projects. The title of the *Festschrift* for Stresemann's 60th birthday, *Ornithologie als Biologische Wissenschaft* (Mayr & Schüz 1949) [*Ornithology as a biological science*], acknowledged this major achievement. It is true that the technical progress during the 20th century (e.g. the availability of advanced photography, slow motion and color film cameras, voice recording equipment, color bands, etc.) facilitated a broadening of research programs in many areas of ornithology, and that numerous additional opportunities for research and positions developed after about 1920, and especially after the Second World War. However, we are here mainly referring to conceptual rather than technical advances. On the occasion of Stresemann's 80th birthday Ernst Mayr (1969) said:

"Despite all emphasis on the freedom of scientific research, leaders are required in science as elsewhere. Ornithology of the 1920s badly needed such a leader. . . . You then opened windows and doors permitting fresh air to blow through the halls of ornithology. . . . That a new

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epoch was opened for ornithology during the 1920s, is owed to your creativity and your efficacy. Not three others would have been able to achieve what you did all by yourself".

In view of the general significance of these developments, Stresemann's influence is here documented in some detail. Although he himself was primarily a systematist and zoogeographer, his interests also included functional morphology, physiology, ecology, and ethology. Living birds and the adaptations to their respective modes of life always interested him deeply. Through his personal intervention and with his characteristic far-sightedness he promoted several new research traditions and the careers of promising young scientists during the 1920s and 1930s as well as the following decades. Although Stresemann was aware of the new developments initiated through his own work and that of his students and colleagues during that time (see Stresemann 1938: 21–22, 1951: 358), he did not discuss this paradigm shift in any detail, perhaps because of personal modesty or because he was still too close to these events when he wrote the manuscript of his book on the history of ornithology (1951, 1975) during the late 1940s.

(1) As the new editor of the *Ornithologische Monatsberichte* [*Monthly ornithological reports*] he published the following *Announcement* in December 1921: "Only by connecting our discipline with all branches of science research will we be able to comprehend the avian organism and many of its biological characteristics. For this reason we will publish in future issues of the *Monatsberichte* detailed reviews of the more important publications in the entire field of ornithology including anatomy and physiology".
(2) In 1922–1923 he invited B. Rensch from Halle and E. Mayr in Berlin (then students aged 22 and 18 respectively, though the former had already completed his PhD) to work in his bird department at the Zoological Museum between semesters. In 1925 he persuaded the medical student Mayr to switch to zoology and to write his thesis under Stresemann's supervision.
(3) Beginning in 1924 he intensified, with O. Heinroth, the exchange of thoughts and opinions among ornithologists in the Berlin region by organizing, besides the public monthly meetings of the *DO-G*, a second more technical monthly meeting of *DO-G* members only, where many new ideas and publications were discussed (see *J. Ornithol*. 72 [1924]: 27l, 567).
(4) During the 1920s and 1930s he supervised studies and dissertations dealing with the physiology and functional morphology ("biological anatomy") of birds, most of them published in the *Journal für Ornithologie*.
(5) A letter to K. Lorenz in 1934 (who was then 30 years old) induced him to quit his position at the Anatomical Insitute in Vienna in order to study animal behavior.
(6) In November 1934 Stresemann invited G. Niethammer (then 26 years old) to come to Berlin and work on the project of the *Handbuch der deutschen Vogelkunde* [*Handbook of German ornithology*], published 1937–1942. In 1962 he persuaded U. Glutz von Blotzheim to take over the editorship of the new *Handbuch der Vögel Mitteleuropas* (1966–1997) [*Handbook of the birds of Central Europe*].
(7) Stresemann's verbal criticism of E. von Holst's ideas on the flight of birds led to the latter's construction of his "artificial birds" (1943; see also *J. Ornithol*. 120 [1979]: 455–456).
(8) In 1946 he invited G. Kramer (then an assistant professor with E. von Holst at the University of Heidelberg) to coedit with him the *Ornithologische Monatsberichte* (the first postwar ornithological journal) and to review certain foreign publications that had appeared during the Second World War. Kramer's critical review (1948) of attempts at understanding the orientation of migratory birds led him to study this problem himself, beginning in 1947.

Through his influence and work, Stresemann instigated a full paradigm shift in world ornithology, the "Stresemann revolution". As mentioned above, ornithologists until the early 20th century were concerned predominantly with problems of the systematics and distribution of birds in different regions of the world, i.e. with topics of systematic ornithology. Problems of general ornithology were hardly ever addressed. The questions posed under the new paradigm, and gradually accepted by ornithologists worldwide, were totally different from the earlier ones and concerned (e.g.) functional morphology, adaptations of birds to their particular lifestyles, physiology, breeding biology, courtship, orientation, and other behaviors. In his IOC presidential address, Ernst Mayr (1963: 28) stressed "the shift of the position of ornithology from being merely a hobby to being a legitimate branch of zoology. Erwin Stresemann has perhaps done more than anyone else to bring about this recognition. The numerous young ornithologists whom he trained, as zoologists, at the University of Berlin, formed the first school of genuine scientific ornithologists".

We may ask in retrospect: what circumstances led to this global paradigm change and how can we explain its occurrence? The coincidence of the following historical factors appears to have been decisive (Haffer 2007a,b; Haffer et al. 2000):

(1) The planning of a *Handbuch der Zoologie* in 1913 in which each group of animals was to be treated from a general biological point of view. Thus the table of contents of the volume on birds, as laid out schematically by the editor W. Kükenthal (1861–1922), was that of a

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handbook of general ornithology with an emphasis on anatomy, ontogeny, physiology, and ecology, including the relations between the bird and its environment (see Fig. 34).

(2) The author was a young zoologist of the next generation not entrenched in the research traditions of the preceding century.

(3) Stresemann perceived his task of writing the manuscript of the *Aves* volume (starting after the First World War in 1919) and his other ornithological activities as a challenge to develop a "New Avian Biology", of which his *Aves* (1927–1934) was to become the "founding document".

(4) As Secretary (1922–1945) and President (1949–1967) of the German Ornithologists' Society, editor of the *Journal für Ornithologie* and of the *Ornithologische Monatsberichte*, and supervisor of many PhD students, as well as in his capacity of senior ornithologist at the Berlin Zoological Museum, Stresemann occupied a central position in German ornithology and, given his personality, was able to effectively influence the type of research conducted, topics discussed at annual meetings, and manuscripts published.

(5) Congenial colleagues like Heinroth, Koehler and Lorenz supported Stresemann's plans and vision. As the most prominent professional ornithologist among these key scientists of the 1920s and 1930s, Stresemann was the prime mover for these new programs, encouraging his colleagues and publishing their work and that of their students in the *Journal für Ornithologie*. Heinroth was director of the Aquarium of the Berlin Zoological Garden and did most of his ornithological work during his spare time. Lorenz conducted behavioral studies in Altenberg, near Vienna, on a private basis until he became Professor of Comparative Psychology in Königsberg in 1940. Kramer (1930) had made behavioral observations in the Zoological Garden of Berlin and later worked at the Biological Station in Naples, Italy, from where he visited Lorenz in Altenberg during the 1930s. During the mid-1930s, Otto Koehler (1889–1974), Professor of Zoology at the University of Königsberg and a friend of Stresemann since their student days in Munich, turned his attention to behavioral studies of birds. With C. Kronacher and K. Lorenz he founded the *Zeitschrift für Tierpsychologie* (today *Ethology*) in 1936. The first volume appeared in 1937. These ornithologists and ethologists remained in close communication with one another over the following decades, when comparative ethology was being developed as a scientific discipline (Festetics 1988; Koehler 1988; Wuketits 1990; Thielcke 1991).

(6) Stresemann's student Ernst Mayr (1904–2005), who had emigrated to the United States in 1931, transmitted ideas and suggestions stemming from the Stresemann circle to several colleagues like Margaret M. Nice, J.J. Hickey and others. He organized in 1933 an ornithological seminar series where current literature was reviewed and especially work on bird behavior and life history studies discussed. Hickey's influential *Guide to Birdwatching* (1943) used many of the suggestions received from Mayr. Through his setting up of the Sanford Hall on the biology of birds at the American Museum of Natural History (New York) in 1948, Mayr also helped to further the establishment of a New Avian Biology in North America (Figs. 35, 36).


HANDBUCH DER ZOOLOGIE

EINE NATURGESCHICHTE DER STÄMME DES TIERREICHES

GEGRÜNDET VON

DR. WILLY KÜKENTHAL

GEHEIMEM REGIERUNGSRAT

WEILAND O. Ö. PROF. AN DER UNIVERSITÄT BERLIN

UNTER MITARBEIT ZAHLREICHER FACHGELEHRTEN

HERAUSGEGEBEN VON

DR. THILO KRUMBACH

SIEBENTER BAND · ZWEITE HÄLFTE

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Prof. Dr. Erwin Stresemann in Berlin

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Fig. 34. Title page of Stresemann (1927–1934).

A modernization of world ornithology in the sense of a paradigm shift probably would have occurred even without the coincidence of the above historical factors. However, such a change would presumably not have started in Germany and not during the 1920s (but one or two decades later), and probably would have taken place less rapidly than it actually happened.

In 1930 Stresemann was elected President of the Eighth International Ornithological Congress (Oxford 1934), when he was only 40 years old. Other Central European ornithologists before and after him who also served as presidents of the IOC were A. Reichenow (1910), K. Immelmann (1986), and P. Berthold (1998), while the following presidents had been born and raised in Germany

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Fig. 35. Erwin Stresemann (right) and Ernst Mayr at the XIVth International Ornithological Congress in Oxford, 1966 (from Haffer et al. 2000).

but lived abroad when they were elected: G. Radde (First IOC in 1884), E. Hartert (Sixth IOC in 1926), and E. Mayr (Thirteenth IOC in l962). In his presidential address in 1934, Stresemann was able to state: "Ornithology is no longer the *scientia amabilis* somewhat disdainfully smiled at by so-called competent general zoologists. We witness nowadays that geneticists, evolutionists, and animal psychologists learn from ornithologists or at any rate are treating us as being of equal rank. Let us rejoice then over this development, which will assure us a steadily increasing influx of university students and thereby help us to obtain a very honorable place in the system of zoology" (1938: 21–22), and later regarding the more recent developments: "The barriers that protected our special field were demolished on all sides. Ornithology has progressed with such breathtaking speed that nothing important can be achieved in it nowadays except by keeping up with the pace, without losing sight of the whole" (1951: 358, 1975: 351).

After Stresemann had taken over the editorship in 1921, the *Journal für Ornithologie* published more and more papers on biological topics like breeding biology, ecology, behavior and feeding habits, thereby becoming the world's leading ornithological journal during the 1930s. The *Journal* set an entirely new style which has been adopted to a lesser or greater degree by most major ornithological journals (Mayr 1963: 28). As Moreau (1959: 33) asserted after spot-checking and comparing the contents of several major journals: the volumes of the *Journal* for "1930 and 1940 were far ahead of the *Ibis* in the range and the maturity of their contributions. Apart from many life-history papers, they dealt with breeding seasons, migration, food, ecology and bio-chemistry". Other topics that were now frequently discussed included functional morphology, orientation, population studies, annual cycles, and – after the sonograph had been developed – bioacoustical work, as well as occasional papers on zoogeography, fossils and evolution, parasites and, during recent years, the effect of environmental contamination with heavy metals.

Comparing the contents of the *Journal* volumes prior to and after 1920 reveals the greater length of many of the early articles, particularly those listing the species represented in bird collections from overseas or observed during an expedition. Also the writing style of the earlier authors was generally more verbose and descriptive compared with that of later contributors. Voluminous descriptive reports from the bird observatories were included in

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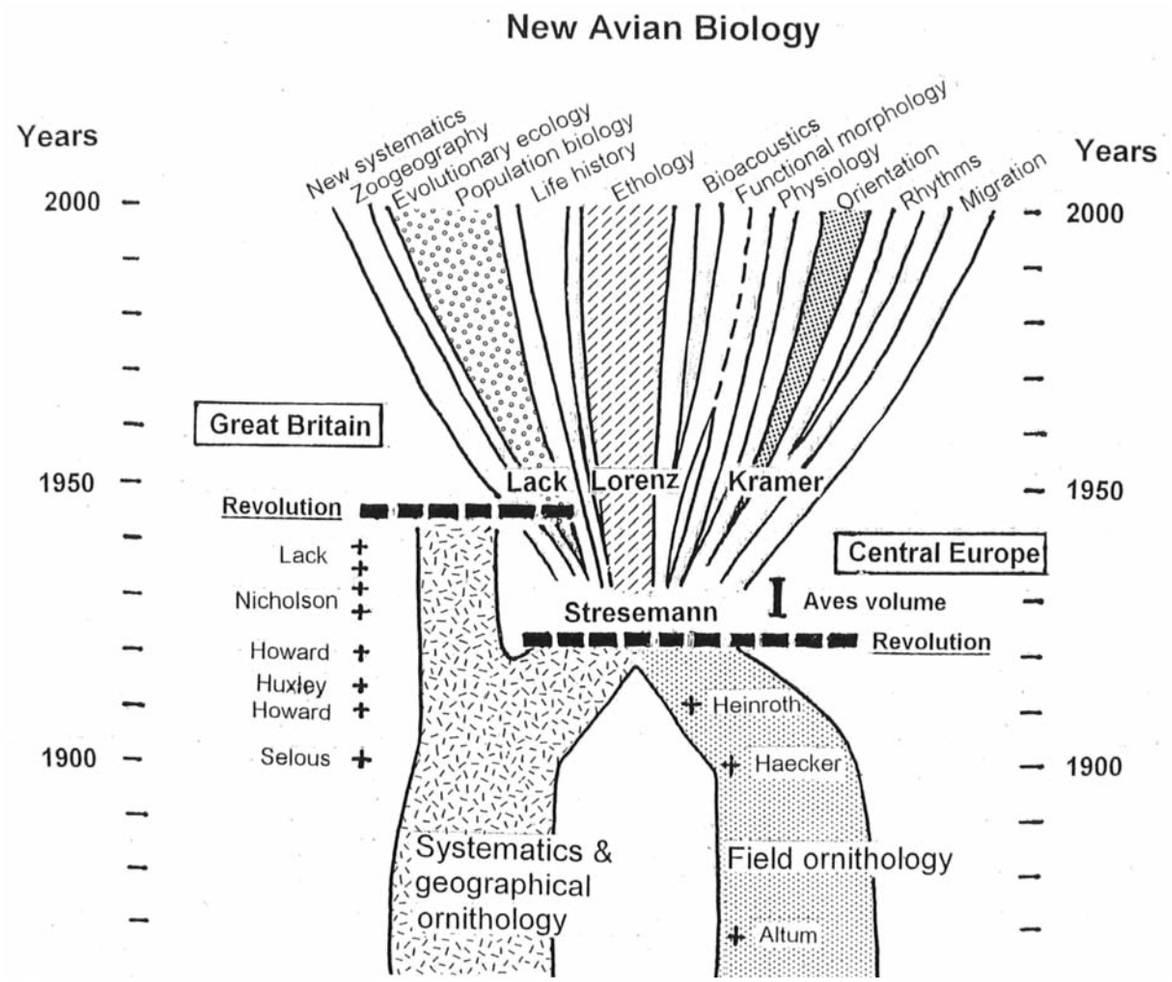

Fig. 36. The "New Avian Biology" 1850–2000.

the *Journal* during the 1870s and 1880s, and again during the first three decades of the 20th century. The number of articles in the three main research topics of the earlier ornithology (systematics, faunistics in overseas countries and in Central Europe) diminished greatly during the l930s. Those that did appear in these fields during that time differed in approach and were based on extended field experience of the authors themselves (e.g. on the avifaunas of Tibet – Schäfer 1938, southwest Africa – Hoesch & Niethammer 1940, and Japan – Jahn 1942). They discussed many ecological and other biological aspects of the bird faunas of these regions. The last work of this type published in the *Journal* was that on the avifauna of western Siberia (Johansen 1943–1961).

Among the topics that occupied early, and a few modern researchers are the study of egg shells (oology) and of plumages and molt. During the 1850s the question was discussed whether or not feathers may change their colors or whether plumage color change is accomplished exclusively through molting (and abrasion). In recent decades Erwin and Vesta Stresemann studied the molt sequence of wing and tail feathers in many groups of birds. Their monograph on *Die Mauser der Vögel* [*The molt of birds*] appeared as a special issue of the *Journal* in 1966.

Functional morphology. Early naturalists like von Pernau and Zorn during the 18th century, C.L. Brehm and many others during the first half of the 19th century, based their observations on the teleological principle (the search for a purpose) which, given the rudimentary state of the sciences, led to fairly accurate conclusions for their times (Stresemann 1975: 293, 302). Through his thoughtful comparative observations and explanations of (e.g.) the climbing structures of the Eurasian Nuthatch and the woodpeckers, Brehm became a precursor of functional morphology. Other pre-Darwinian naturalists also made excellent observations on the structure and habits of birds until, after 1859, Darwin's theories diverted the attention

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of ornithologists (and zoologists in general) to historical studies of homologies and the evolutionary relationships of different groups of birds. However, Fürbringer's (1888) and Gadow's (1891, 1893) large volumes are of equal importance to comparative and functional morphology. A revival of functional studies took place in Germany during the early 20th century through the work of Hesse & Doflein (1910, 1914) on the structure and life of animals, Virchow (1918) on the spinal column of the Common Crane, and especially that of the anatomist and ornithologist Hans Böker (1886–1939), who called attention to the direct relationships between environment, behavior, and the morphology of organisms (1935, 1937). Probably at Stresemann's suggestion, Böker held a lecture at the annual ornithological meeting in 1924 on the evolution of bird flight that was published under the title *The biological anatomy of types of bird flight and their evolution* (1927).

Stimulated by the ideas of these workers and based on his work on the manuscript of the *Aves* volume, Stresemann instigated and supervised a large series of dissertations on avian morphology, embryology, histology, physiology, bird flight, feather structure, and coloration with a functional perspective, most of them published in the *Journal für Ornithologie* during the 1930s (the full titles of these dissertations and references are listed in *J. Ornithol.* 114 [1973]: 498–499). However, no Stresemann "school" of functional morphology developed because as a museum scientist he was unable to place his students in university positions, essential for the development of such an entity. Only Hans Scharnke (1907–1941), the most active and promising student in this field, became an assistant professor at the University of Munich, but died soon after in the Second World War. During later decades further topics studied by the following generations of ornithologists concerned the functional morphology of the avian head (Hofer, Barnikol), the oscine jaw muscles (Fiedler), the avian jaw apparatus (Bühler), respiration (H.-R. Duncker), ontogeny of birds (M. Starck), functional morphology of feathers (E. Rutschke), the feathering and bones of the wing (B. Stephan), and the flight of birds (H. Oehme, W. Nachtigall, G. Rüppell). Two workers in Central Europe, contemporaries of Stresemann, who published excellent functional studies during the course of the 20th century, were Hans Steiner (1889–1969) and his students in Zürich (e.g. V. Ziswiler, and his student in turn D. Homberger), and Adolf Portmann (1897–1982) and his students (especially E. Sutter) in Basle.

When H. Ruska had published the first electron-microscopical images of biological objects during the 1930s, Stresemann suggested to his doctoral student F. Frank to apply this new technique to his study of the coloration of bird feathers. This led to Frank's discovery of the structures causing the blue color of feathers (Frank & Ruska 1939), although its detailed physical basis was only clarified later (Schmidt & Ruska 1962). This first application of the electron microscope initiated a new research tradition for the study of the iridescent feather coloration of hummingbirds, peacocks, sunbirds, trogons and starlings (Durrer 1962; Durrer & Villiger 1962, 1966, 1970), of birds of paradise and ducks (Rutschke 1966, 1972), and other birds (Dyck 1976). Otto Völker (1907–1986) analyzed the biochemical composition and physical properties of feather pigments in a series of papers, many of which appeared in the *Journal für Ornithologie* between the 1930s and 1950s (summarized by Völker 1963, 1965). The latter research tradition had been initiated by Altum (1854) and Bogdanow (1858) and was continued by the work of Valentin Haecker and several of his students between 1890 and l924, reviewed by Immelmann (1965).

Since the mid-1970s, a number of ornithologists have pursued ecological aspects, investigating the adaptiveness of morphological features, the partitioning of resources by species, aspects of evolution, and the diversity of taxonomic groups. Ecomorphological research requires full knowledge of the functional and adaptive significances of the features studied, such as bill, leg, and wing (Winkler 1989; Bock 1990b). H. Winkler and B. Leisler combined behavioral observations with experimental and morphological approaches, studying woodpeckers, migratory songbirds, reed warblers, weaver finches and kingfishers (Winkler & Bock l976; Bock 1977; Leisler 1977; Leisler & Winkler 1985, 1991; Winkler & Leisler 1985, 1992; Leisler et al. 1987, 1989, 1997; Ley 1988; Winkler l990).

Physiology. In 1924, comparative studies by V. Haecker, Professor of Zoology at the University of Halle, indicated that the readiness of a bird to sing is probably related to the development of its gonads, i.e. it depends on the production of sexual hormones. He also discovered (1926, 1927) differences in the histology and size of the thyroid gland of a crow during the course of the year (small during spring and early summer, large during fall and winter, i.e. in reverse order to the annual size changes of the gonads). An increased assimilation through an increase in thyroid activity in birds under low ambient temperatures during migration and molt was later confirmed (see Immelmann 1965). Haecker (1916, 1924) also studied the light-dependence of the beginning and end of song in different bird species in the morning and evening. He already noted that songbirds begin singing in the morning in weaker light conditions than when they stop singing in the evening (when the variation is also more pronounced).

Physiological topics investigated by Stresemann's students included the "Physiology and acoustics of avian vocalizations" (Rüppell, *J. Ornithol*., 1933), "The effects of bacteria in the intestines of birds" (Putzig 1934), and "Annual changes in the histology of the thyroid gland in birds" (Küchler, *J. Ornithol*., 1935). In his major textbook, Groebbels (1932, 1937) emphasized ornithological stud-

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ies from a physiological-biological viewpoint and attempted to uncover the functional relationships between the bird and its environment. His work therefore effectively supplemented Stresemann's *Aves*. After the Second World War, Berger studied the physiology and energetics of bird flight (Berger & Hart 1974), Jacob (1982) the occurrence and function of stomach oils, Jacob & Ziswiler (1982) the structure and function of the uropygial gland, Schwartzkopff (1973) the physiology of hearing in birds, and Berthold (1975) the physiology of bird migration. Prinzinger (1990, 1996) and his school analyzed energy metabolism in birds and other animals. He established the surprising fact that physiological time is nearly identical for all birds regardless of mass, when expressed as "energy metabolism per gram". Measured in (mass-specific) physiological time units, all birds, mammals and other animals have about the same duration of their different life stages and, in this sense, have identical life spans.

Ethology and breeding biology of European birds. When the German Ornithologists' [Ornithological] Society *DOG* celebrated its 50th anniversary in 1900, Herman Schalow (1852–1925) reviewed the progress made, especially with respect to the knowledge of taxonomy and distribution of European and non-European birds. He ended his presentation with the following vista into the future: In the years to come "the habits and life histories (of birds) should be studied. . . . Important tasks will then be (1) to watch these highly organized birds in their instinctive daily activities, (2) to recognize the relations between an individual bird and its social environment, and (3) to make an attempt at perceiving and understanding the independent, peculiar actions of individual animals in particular circumstances. We will then have to examine in which way the behavior of birds, usually considered as the result of an inexplicable instinct, may be explained. . . as a sensible utilization of sensory perceptions" (1901: 24–25).

With this remark Schalow probably referred to the then still unresolved controversy between the views of the Altum group versus those around A.E. Brehm. An author who resisted the usual anthropomorphic interpretation of bird behavior during those years was Valentin Haecker (1864–1927). In discussing the song of birds (1900) he attempted a comparative treatment of song instincts within a Darwinian framework, concluding that sound quality and rhythm are innate, but that the details of the song (of Chaffinch and Nightingale) are learned from other males, usually the father. According to Haecker, the biological functions of bird song are recognition of conspecific birds as well as attraction and stimulation of females. However, he did not mention the third important function, that of territorial advertisement directed at other males, which had been discovered by Altum (1868), though Haecker probably did not know this book. In comparative discussions, he suggested the possible evolutionary development and differentiation of various song types from simple calls, of instrumental vocalizations (e.g. drumming of woodpeckers and the drumming-flight of snipes), of song-flights, courtship behavior, and of some general behavior patterns of birds like ruffling of feathers, drooping of wings, and spreading of tail feathers. He separated simple reflexes from more complex instincts; see Immelmann (1965) for a review. The first "psychological" article published in the *Journal für Ornithologie* was a long paper by Groebbels (1910), who also treated the development of bird song from a Darwinian point of view. He emphasized the previous neglect of "ornitho-psychological" topics despite their general biological importance, and distinguished between (1) the anthropomorphic interpretation (e.g. A.E. Brehm), (2) the metaphysical interpretation (e.g. Altum), and (3) the evolutionary interpretation of behavior patterns in animals (e.g. Darwin, Haecker).

The ornithologist in Germany who initiated the comparative study of behavior (ethology) as a branch of zoology was Oskar Heinroth (1871–1945). As a boy he had been stimulated by *Brehms Tierleben* to observe motor patterns, especially in the courtship behavior of ducks and geese (like Haecker, he apparently did not know Altum's book of 1868). Heinroth continued to pursue ornithological activities while he was a student of medicine and later zoology, when he learned about Darwin's theories. After his return from an expedition to the Bismarck Archipelago (1900–1901) he became an assistant to the director of the Berlin Zoological Garden in 1904 and then Director of the Aquarium there in 1913, a post which he held until his death in 1945 (K. Heinroth 1971; Mauersberger 1994b).

When the Fifth International Ornithological Congress convened in Berlin in 1910, Heinroth summarized his long-term observations on the behavior of ducks and geese in a major presentation, a milestone in the comparative analysis of instinctive behavior in animals within a Darwinian framework. He described constant innate behavior patterns which, like morphological structures, characterize certain taxa (species, species groups within genera, genera, families) and indicate closer or more distant evolutionary relationships.

This paper, published in a congress proceedings (1911) with rather restricted distribution, was virtually without any effect on other ornithologists until Oskar and Magdalena Heinroth began to publish another major work: *Die Vögel Mitteleuropas in allen Lebens- und Entwicklungsstufen photographisch aufgenommen und in ihrem Seelenleben bei der Aufzucht vom Ei ab beobachtet* (4 vols. 1924-1933) [*The birds of Central Europe photographed in every stage of life and development and observed in their behavior from the egg onward*]. Beginning in 1904, the Heinroths (that is, mainly Magdalena) had hand-reared individuals of almost all Central European species from the egg and observed their development in order to determine to what extent the behavioral char-

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acters (including vocalizations) of a given species are innate or have to be learned by the young bird after hatching. In these volumes they emphasized "details of habits, growth and development, feather change, instinctive behavior patterns (*Triebhandlungen*) and psychological faculties, i.e. aspects which so far have been seldom taken into consideration" (Heinroth & Heinroth 1924: IX). A detailed presentation of Heinroth's theoretical views and his contributions to the development of ethology is included in the "Russian manuscript" of Lorenz (1992; see also Podos 1994 and Burckhardt 1990, 1999). Stresemann (1975: 347) concluded that Heinroth's work was the first step toward bridging the gap between avian systematics and avian biology, the two major branches of ornithology.

During the 1910s both Heinroth and Stresemann had realized that the data summarized by the authors of the 19th century represented only a beginning of an understanding of the life histories of even the common birds of Europe. Much additional work was needed to complete this task. Stimulated by the work of the Heinroths and encouraged by Stresemann as Secretary of the *DO-G* and editor of the *Journal für Ornithologie*, many ornithologists in Europe began to observe in detail the nest-life, habits and growth of birds. The bi-weekly *DO-G* meetings organized by Heinroth and Stresemann in Berlin during the 1920s and 1930s also helped to spread the new ideas. Numerous excellent and well-illustrated contributions on the breeding biology of various species appeared in the *Journal,* such as those of G. Schiermann on Savi's Warbler (*Locustella luscinioides*, 1928*)* and Little Crake (*Porzana parva*, 1929), H. Siewert on raptors (1928, 1930, 1932, 1933, 1941), R. Dircksen on terns and oystercatchers (1932), F. Goethe on Herring Gull (*Larus argentatus*, 1937), or O. Steinfatt on the Spotted Flycatcher (*Muscicapa striata*, 1937), Woodcock (*Scolopax rusticola*, 1938), Fieldfare (*Turdus pilaris*, 1941), and Tree Pipit (*Anthus trivialis*, 1941). The new periodical *Beiträge zur Fortpflanzungsbiologie der Vögel* (1924–1944) [*Contributions to the reproductive biology of birds*], ably edited from 1926 onward by Ludwig Schuster (1883–1954), also encouraged this line of research, at the same time transforming several previous egg-collectors into ornithologists (the earlier *Zeitschrift für Oologie* had ceased to appear in 1924). Early disks with the songs of about 50 bird species recorded by Ludwig Koch (1881–1974) were published by Heinroth and Koch in 1935–1936 entitled *Gefiederte Meistersänger. Das erste tönende Lehr- und Hilfsbuch zur Beobachtung der heimischen Vogelwelt* [*Feathered mastersingers; the first self-teaching audio book for the observation of our birds*]. Earlier, A. Voigt (1852–1922), C. Schmitt (1874–1958), and H. Stadler (1875–1962) had dealt with graphical methods of the representation of bird voices (Schmitt & Stadler 1919; Wallschläger 1982).

Jacob von Uexküll (1921, 1934), studying the interrelationships between organisms and their environment, demonstrated that the sense organs of animals fit their surroundings and that only such objects and signals which possess some significance for the life of the animal are perceived. Konrad Lorenz (1903–1989) investigated the social behavior of Jackdaws at his family estate near Vienna (Austria) when, in 1924, he learned about the work of the Heinroths. He wrote to them immediately, and their close correspondence from 1930 to 1940 was published by O. Koenig in 1988. In his early papers on bird behavior published in *Journal für Ornithologie* – Observations on Jackdaws 1927, Contributions to the ethology of social corvids 1931, Species-specific instinctive behavior patterns 1932, Bird flight 1933, The companion in the bird's world 1935 – Lorenz tried to combine the findings of Heinroth and von Uexküll with his own results. Lorenz had also been corresponding with Stresemann since the late 1920s and even asked for his advice regarding his future career. When in 1934 the director of the Anatomical Insitute in Vienna, where Lorenz held an assistantship, retired and his successor did not permit him to continue his previous part-time ethological studies, Lorenz (then 30 years old) turned to Stresemann "as a real friend". His reply reads as follows:

"My dear Dr. Lorenz, Berlin, 7 March 1934
In view of the new situation there can be no doubt concerning your decision. You must give up anatomy. Your talents in the fields of animal psychology are so prominent that it would mean an autotomy (and in addition a biologically detrimental one!) if you were now to be intimidated and act 'rationally' instead of instinctively. When the instinctive side is so conspicuously developed in a person as it is in your case, he should be happy about this gift of God. Don't worry and plunge into the water like a young guillemot, you will surely be able to swim. If it somehow means an alleviation to you, you are welcome to pass much of the responsibility on to me, I bear it with pleasure, . . . In full confidence for you. Yours (E. Str.)".

Thus Konrad Lorenz continued to analyze species-specific motor patterns and the social behavior of birds and other vertebrates. Many examples came from the ducks and geese, Heinroth's favorite groups. He summarized the results of his studies into the evolutionary relationships of ducks based mainly on their courtship movements in the *Festschrift* published on the occasion of Heinroth's 70th birthday (1941).

Another founder of comparative ethology was Otto Koehler (1889–1974); see Hassenstein (1974) and Thielcke (1991). After he had studied the behavior of *Paramecium* during the 1920s, he and his students observed the breeding behavior of individually marked Ringed Plovers (*Charadrius hiaticula*) and Lapwings (*Vanellus vanellus)* on the Baltic coast, also conducting experiments on egg-

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rolling and orientation to the nest site (Koehler 1941; Laven 1941). In the laboratory, the former analyzed the ability of birds to count (1955) and the development of song, mainly in Blackbirds (*Turdus merula*), with conclusions on bird song as a first step towards music and language (1951) and pre-verbal thinking in animals (1956). Besides ethograms of numerous bird species and other vertebrates, major topics of ethology in the following decades were structure and meaning of vocal performances, song learning, imitation and dialects, courtship and territory, enemy recognition, development and neural mechanism of behavior (e.g. Löhrl 1960–61, 1964; Thielcke 1968, 1970; Nicolai 1970; Curio 1976; Bergmann & Helb 1982). The phenomenon of imprinting first studied by Lorenz was further analyzed by Immelmann (1935–1987) and his school (Immelmann et al. 1996). He also studied ecological aspects of the periodic reproduction of birds in non-uniform environments, in particular the proximate and ultimate control of reproduction, such as food supply, predation, endogenous periodicities, or environmental and social stimuli (Immelmann 1971).

Migration and orientation of birds. The phenology of long distance migration has interested a host of ornithologists for over two hundred years (R. Wiltschko 1989). During the late 19th century, efforts were made to record and map the movements of migratory birds in Central Europe (twelve annual reports were published in the *Journal für Ornithologie* 25 [1877] to 40 [1892]). The first International Ornithological Congress in Vienna (1884) was to some extent established in order to set up a network of European sites to monitor migration, but it came to nothing due to the difficulties of analyzing the collected data (Haffer 2007a).

As early as 1859, Middendorff suggested that birds use the magnetic field of the earth as a means of orientation. General summaries of the phenomena involved, like migration "routes", speed and height of flight during migration, possible means of orientation by diurnal and nocturnal migrants were published by E. von Homeyer (1881) and Gätke (1891), the latter after having observed bird migration on the island of Helgoland since 1837. After bird-banding schemes had been established at the newly founded observation stations in Rossitten (today Rybachiy in Russia) in 1901 and on Helgoland in 1910, annual reports were published in the *Journal für Ornithologie* until 1924, during which period the study of bird migration was boosted considerably (Lucanus 1922; Thienemann 1927, 1930). After the Second World War, the work of the observatory of Rossitten was transferred to Radolfzell (Bodensee/Lake Constance). Atlases based on the banding and recovery reports appeared in 1931 (Schüz & Weigold), in 1975-1985, and 1995 (Zink; Zink & Bairlein). More recent summaries of bird migration studies are those of Schüz et al. (1971) and Berthold (1990b), which include the results of radar observations introduced by Sutter (1957).

The well-planned and successful displacement studies of W. Rüppell (1935, 1937) initiated the experimental analysis of orientation behavior of migratory birds. During recent decades, laboratory experiments have established that the direction and duration of movements in many birds are based on endogenous programs. Markers for orientation probably are the sun (Kramer, Schmidt-Koenig), the stars (Sauer), and/or the magnetic field of the earth (Merkel & Wiltschko 1965); see also Schmidt-Koenig (1979), Berthold (1991), Wiltschko (1995), Wiltschko & Wiltschko (1995, 1999). To compensate for the apparent movement of the sun and the stars across the sky, migratory birds use an endogenous "clock" and in this way are able to maintain certain compass directions (Kramer, Hoffmann). Internal and external *Zeitgeber* (Aschoff) for circadian and circannual rhythms constitute the mechanism of the "clock" and also regulate breeding and molting cycles (Gwinner 1975, 1986, 1990; Berthold 1996).

The "knowledge" of the distance to be traveled in the genetically determined direction probably results from an endogenously determined amount of energy. When these reserves have been consumed the bird has reached its winter quarters ("vector navigation"), as already suggested on the basis of theoretical considerations without experimental proof by several earlier authors:

"The migrating bird does not need guidance, as it merely follows an instinct which automatically prescribes the direction. . . . The bird does not endeavor to reach a particular goal; instead, the goal of the journey results by itself when the migration instinct ceases" (Lucanus 1922: 132, 134; see also Stresemann 1927–1934: 692, 704).

Meanwhile these suggestions have been confirmed through quantitative measurements of the energy used by caged birds – of various species wintering in different areas – during the period of their "migratory restlessness" (*Zugunruhe*) of differing durations, and the flight directions that they had maintained (Gwinner 1968, 1990). Two-way selective breeding experiments with warblers indicated a high influence of genetic factors for the control of migration habits and yielded large selection responses (Berthold et al. 1990, 1992). These results suggest the potential for a rapid microevolution of migratory behavior in the event of environmental changes.

Population biology of European birds. When Margaret Morse Nice (1883–1974) visited Berlin and the Zoological Museum in early 1932, Stresemann was fascinated by the description of her population studies of the Song Sparrow (*Melospiza melodia*) using individually marked birds near her home in North America. He encouraged her to write up the results obtained so far and published them in German in the *Journal für Ornithologie* (1933–1934), sev-

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eral years prior to the publication of the two volumes of her famous monograph in the United States (1937–1942). As IOC President, he invited her to give a paper at the forthcoming Eighth International Ornithological Congress in Oxford (1934) and encouraged similar studies in Germany.

Gottfried Schiermann (1881–1946) had an unusual ability to locate nests: "One day, just going through the woods with him, he discovered 54 occupied bird nests with me" (Mayr 1997a). He determined the population density of all species inhabiting various forest types around Berlin by counting the nests of each species in his study sites (Schiermann 1930, 1934, 1942–43). Ecological and population studies were later conducted on raptors by (e.g.) Uttendörfer and co-workers (1939, 1952), Schnurre (1935–38), and Wendland (1952–53, 1984).

Observations of color-banded birds were made on the Ringed Plover (*Charadrius hiaticula*) on the shore of the Baltic Sea (Koehler 1941), the Yellow Wagtail (*Motacilla flava*) on Helgoland (Drost 1948), the Yellowhammer (*Emberiza citronella*) near Munich (Diesselhortst 1949, 1950), the Whincat (*Saxicola rubetra*) near Heidelberg (Schmidt-Koenig & Hantge 1954), and the Kentish Plover (*Charadrius alexandrinus*) on the island of Oldeoog (Rittinghaus 1956). A long series of population studies of hole-nesting birds was initiated by Berndt & Frieling (1939) and continued after the Second World War by many workers (e.g. Creutz 1955 and Winkel 1989). Bezzel's book on *Vögel in der Kulturlandschaft* (1982) [*Birds in the man-made landscape*] includes a comprehensive discussion of the results of modern population studies of central European birds, such as data on density and abundance, age composition, mortality and recruitment, distribution patterns and dynamics. In recent years, P.H. Becker marked Common Terns (*Sterna hirundo*) with passive transponders to obtain data on population dynamics (e.g. Wendeln & Becker 1998).

The modern bird census programs and atlas projects permit quantitative estimates of distribution and population trends for many species of European birds.

Relations between aviculture and ornithological research

The keeping and breeding of non-domesticated birds in cages (aviaries) and at ponds in parks has a long tradition in Central Europe, starting in the Middle Ages (Lauffer 1939), and was widespread when von Pernau (1660–1731) studied local birds at his home, even experimenting with some of them. He published his influential book in 1702 (Stresemann 1925, 1951; Thielcke 1988). Almost a century later, J.M. Bechstein issued a *Naturgeschichte der Stubenvögel* (1794) [*Natural history of cage birds*] which appeared in several German and English editions during the following decades. The keeping of cage birds was very popular in many parts of Central Europe during the first half of the 19th century, when C.L. Brehm published the *Handbuch für den Liebhaber der Stuben-, Haus- und aller der Zähmung werthen Vögel* (1832) [*Handbook for lovers of cage birds and all birds that can be usefully tamed*]. Its attraction increased during the second half of the 19th century because of the growing importation of cage birds from overseas. The comprehensive publications by A.E. Brehm on *Gefangene Vögel* (1870–1876) [*Captive birds,* 2 volumes] and K. Ruß on *Fremdländische Stubenvögel* (1870–1876) [*Exotic cage birds,* 4 volumes] furthered the wide distribution of bird-keeping in Europe. These activities of bird fanciers increased scienctific knowledge on the plumages and molt of young and adult birds of many foreign species, as well as details of their general behaviors and breeding biology. The experiences gathered by bird fanciers when keeping "simple" and "difficult" species in captivity were the foundation of several important research traditions during the 20th century:

(1) In the 1920s, Hans Duncker (1881–1961) actively sought to engage bird-keepers in scientific research to investigate the genetics of plumage color (Duncker 1923, 1924; Birkhead et al. 2003);
(2) The ethological studies of O. & M. Heinroth, K. Lorenz, H. Löhrl, J. Nicolai, E. Thaler, K. Immelmann and others who themselves gathered additional avicultural experiences;
(3) The experimental work on song development in songbirds (Thielcke, Messmer, and others);
(4) The experimental studies of G. Kramer, F. Sauer, F. Merkel, W. & R. Wiltschko, E. Gwinner, and P. Berthold on the orientation of migratory birds, on circadian and circannual rhythms, as well as on the physiological and genetic basis of migratory behavior in birds.

The successes of these recent research traditions were unthinkable without the long avicultural tradition in Central Europe (Löhrl 1989). The *DO-G* therefore supported in official statements the lawful keeping and breeding of cage birds (*J. Ornithol.* 119 [1978]: 131 and 128 [1987]: 401–402). However, there exists no historical treatment of European aviculture documenting the beginning, expansion, and decline of the keeping of cage birds as a popular pastime together with remarks on the increase in experience of handling, feeding and breeding of such birds. Regarding the history of the domesticated Canary and its races see Stresemann (1923, 1952), also Birkhead (2003) and Birkhead et al. (2003); on other domesticated birds see Bezzel & Prinzinger (1990: 514–516) and Birkhead & van Balen (2008). Lauffer (1939) mentioned some early records of cage birds in medieval reports and described aspects of aviculture in Thüringen during the 20th century. The paintings of 17th and 18th-century artists docu-

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ment various species of European birds in cages. In 1794, 72 species of cage birds from overseas were kept in Central Europe; this number had increased to 230 in 1870 and to 1450 species in 1920 (Bezzel & Prinzinger 1990: 515). Additional publications refer to the relationships between man and birds in the Harz uplands (Knolle 1980), the Erzgebirge (Gränitz 1981), and in the Oberbergisches Land (Fastenrath-Brunohl 1936), but an overall treatment is lacking. Wille & Spormann (2008) give a very comprehensive recent account of the Harz Chaffinch-singing competitions.

Applied ornithology

Here, applied ornithology comprises both bird protection and the prevention of damage by birds. Barthelmess (1981) published a thorough and enjoyable historical monograph on these topics. We will concentrate in this section on the first of these.

In the millinery trade, the fashion of wearing feathers, wings, or entire bird skins on ladies' hats disappeared during the early 20th century as a result of worldwide protests against the destruction of whole populations of birds of paradise, herons, egrets, grebes, etc. The organized bird protection movement in Central Europe was initiated after 1850 by the publications of Gloger (1858a,b; 1865), Altum (1872, 1877, 1878, 1879, 1889), and K.T. Liebe (see Hennicke 1893), who furthered the general idea of bird protection and mobilized favorable public opinion. The IOC also played an important role in this area. The question of bird species being "useful" or "harmful" was at the center of the discussion. Altum based his opposition against the negative attitude toward raptors and owls on his entomological experience and the results of his ecological studies of the food of many of these birds. Liebe also demanded a reasonable protection of raptors based on his view of nature as a harmonic whole where these birds have their role too. No animal is "useful" or "harmful" he said. Bau (1905) presented a clear and sensible summary of these discussions during the late 19th century, which in many cases had more of an emotional than a technical basis. Local bird protection associations developed from 1870 onward; the German *Bund für Vogelschutz* was founded in 1899 and the *Schweizerische Bund für Naturschutz* in 1909.

Like most of the above scholars, Hans Freiherr von Berlepsch (1899), a cousin of Count von Berlepsch, emphasized the decrease of many bird species because of the decreasing availability of suitable habitats in Central Europe (rather than because of active persecution by man) and recommended many corresponding measures. The best way toward a general bird protection appeared to be via landscape protection. Important ornithological baseline data for such an ecological approach were presented in the books of Jäger (1874), Schnurre (1921), Groebbels (1938), Noll (1941–1942), and Bezzel (1982), as well as by the studies of the food of raptors by Uttendörfer and colleagues (1939, 1952); see also Niethammer (1951, 1963).

Economic bird protection as an aid against insect plagues originally envisioned a direct influence of insect-eating birds and therefore recommended an artificial increase in their population densities. However birds proved ineffective once an infestation had broken out, though they may be prophylactically effective (especially species of Paridae) through their destruction of eggs and larvae during the winter months (Bruns 1963). The initiatives of influential personalities and private organizations led to the realization that long-term studies based on scientific methods were necessary to resolve the multiple connections between individual ecological factors and functions. Quantitative data on the population dynamics of European songbirds over recent decades indicate negative trends in population size for 20 species; only 4 species showed positive trends and 11 had quasi-stable populations (Berthold 1990a; Berthold et al. 1999). See especially Bauer et al. (2005).

Bird artists

Although bird artists are not researchers, their work has always been intimately connected with that of ornithologists (Murr 1938; Mengel 1980; Nottmeyer-Linden 1994; Schulze-Hagen 2000). For this reason the names of the more important bird artists are mentioned here (for details see Anker 1938, Nissen 1953, and Jackson 1999). The Frisch brothers (and one of the sons) prepared many pleasing illustrations for their father Johann Leonard Frisch's *Vorstellung der Vögel in Teutschland* (1733–1764) [*Birds in Germany*], most of which were based on observations of living birds. This was also the case in several historically interesting collections of bird paintings of the 18th century which never found a publisher: (1) *Aviarium prussicum* by J.T. Klein (1685–1759), comprising the paintings of S. Niedenthal, is preserved in Erlangen; (2) J.C. von Mannlich's (1741–1822) *Sammlung europäischer Vögel* [*Collection of European birds*] originally contained more than 300 excellent plates, only a few which could be traced (Schlenker & Baumeister 1995); (3) the numerous excellent paintings of Georg(e) Forster (1754–1794), writer, naturalist and geographer, which he prepared as assistant to his father J.R. Forster (1729–1798) during Captain James Cook's second Pacific expedition (1772–1775) and which are now at the British Museum and in several archives (Steiner & Baege 1971; Whitehead 1978; Forster 2007).

A. Gabler and J.M. Hergenröder provided excellent illustrations for J. Wolf & B. Meyer's *Naturgeschichte der*

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Vögel Deutschlands (1805–1821) [*Natural history of the birds of Germany*]; see Schlenker (2000). Their work reached the quality of the realistic and magnificent plates of J.F. Naumann, who was simultaneously author and artist of the most celebrated German ornithological handbook published during the 19th century. J.C. Susemihl began to paint the plates for Bor[c]khausen's *Teutsche Ornithologie* in 1795, almost at the same time as Naumann started the illustrations for his father's *Naturgeschichte.* The Germany of the first half of the 19th century did not have the connections with tropical countries which Britian and France had, which is why very few illustrations of the colorful birds inhabiting equatorial regions appeared there during the first half of the 19th century (e.g. in the works of Spix 1824–1825 and Rüppell 1845).

Joseph Wolf (1820–1899) was equally able to portray a bird in a scientifically accurate manner and in a pleasing way from an artistic point of view. He was born in the Eifel region and even as a young man contributed excellent illustrations to the books of E. Rüppell (Frankfurt a. M.), J.J. Kaup (Darmstadt), and H. Schlegel (Leiden) between 1839 and 1847. He continued his career in London, becoming the greatest animal painter of the 19th century (Schulze-Hagen & Geus 2000). F.W.J. Baedecker (1788–1865) published beautiful plates illustrating the eggs of European birds (1855–1867), while his equally outstanding bird paintings remained unpublished (Baege 1969). Other bird artists of the 19th century include R. Kretschmer, F. and A. Specht, W. Heubach, W. Kuhnert, and G. Mützel, who also painted many representatives of other animal groups. The poorly reproduced chromolithographic plates accompanying the second edition of Naumann's work (1897–1905) were based on the high-quality paintings of B. Geisler, A. Göring, O. Kleinschmidt, O. von Riesenthal and others. E. Aichele and W. Heubach illustrated O. Fehringer's *Die Vögel Mitteleuropas* (1922–1931) [*The birds of Central Europe*]. O. Kleinschmidt's bird paintings with which he illustrated his books on the songbirds (1913) and raptors (1934) of Germany, as well as those of his monograph series *Berajah* (1905–1937) are well executed and excellently reproduced. Other Central European artists of the 20th century include O. Natorp, H. Kirchner, F. Murr, and F. Weick and W.D. Daunicht, the last two distinguished by their painstaking work for the immense *Handbuch* of Glutz von Blotzheim and Bauer (1966–1997).

Ornithological research centers in Central Europe

Public and private natural history museums and collections were the centers of ornithological research during the 19th century, when very few salaried ornithological positions existed. Besides professional ornithologists at the public museums, private scholars advanced systematic ornithology and influenced young scientists and their careers in Europe. As an example we can mention Hans Count von Berlepsch (1850–1915), who actively encouraged and supported E. Hartert, K. Jordan, and O. Kleinschmidt during the 1890s and the young C. E. Hellmayr from 1900 onward. Walter Rothschild employed Hartert at his private museum in Tring, England in 1892. During the early 20th century, the museums of Vienna, Bonn, Dresden, and Frankfurt a. M. took over the private collections of V. von Tschusi zu Schmidhoffen, A. Koenig, O. Kleinschmidt, and Count Berlepsch respectively, where (together with other materials) they continue to be available for modern research on systematics, geographical variation, and zoogeography.

During the decades following the Second World War the emphasis of ornithological research gradually shifted away from the museums to large laboratories at the universities and other institutions, with studies of the ontogeny of behavior patterns, the phenomenon of imprinting, the genetics of migration, or the mechanisms of orientation and navigation in migratory birds. Research at the universities is carried out at zoological institutes and depends on the scientific interests of the respective professor. It is therefore less formalized and less continuous than at museums and similar institutions. Some universities nowadays offer introductory and advanced courses in ornithology.

Most state institutions dedicated to ornithological research were founded to study bird migration or applied problems of bird protection. While these objectives continue to be pursued, most of these institutions now include in their programs other aspects of the biology of birds.

Natural history museums and their bird collections have important roles to play in current programs. They document the occurrence of common, rare, threatened, and extinct species and continue to provide the basis for much modern research, especially using molecular genetic techniques (e.g. Berlioz 1960; Miller 1985; Remsen 1995; Mearns & Mearns 1998: 393 ff.; Collar et al. 2003; Rheinwald 2003; Roselaar 2003; van den Elzen et al. 2005; Joseph 2011; Frahnert et al. 2013). In addition, many museum scientists study live representatives of their specialty groups in the field and/or in aviaries. Systematic surveys of particular groups of birds worldwide, or handbooks of the avifauna of a particular region, are prepared with constant reference to museum collections. The illustrations in modern field guides are painted on the basis of museum specimens, and we all carry with us into the field "miniature bird collections" transformed by artists and scientists into identification books. The current research on biodiversity is a joint effort by zoologists of different spezializations (including museum workers), demonstrating again the continued importance of museum collections.

Traditionally ornithologists, like other scientists, have been men. This imbalance has been remedied to some extent only recently. Even in earlier times a few outstand-

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ing Central European female travelers and scientists advanced the cause of ornithology, like Ida Pfeiffer (1797–1855), who collected on Madagascar and many other parts of the world, Amalie Dietrich (1821–1891), who sent birds and other animals (as well as plants) from Australia to Germany, Dr. Emilie Snethlage (1869–1929), who studied the bird fauna of Amazonia, and Dr. Maria Koepcke (1924–1971), who worked on the birds of the lowland deserts and forests as well as the Andes mountains of Peru.

Bird-banding programs during spring and autumn migration periods continue with the help of numerous volunteers among non-professional ornithologists. Many of these also dedicate themselves to other avifaunistic work at more sophisticated levels than their predecessors in former times. The results of their work represent the quantitative database for long-term studies and for detailed distribution atlases at local, regional, or international levels. Many ornithologists without an institutional affiliation conduct studies on the breeding biology, ecology, food habits, or molt of selected species. Most members of local and national ornithological societies and formal working groups are non-professional ornithologists. On a percentage basis, the number of articles published by non-salaried ornithologists (amateurs) in the national journals has decreased since the Second World War while, at the same time, those of university-trained ornithologists have increased. This is a result of specialization, improved education levels, augmented funding, and increased numbers of professional ornithologists at research institutes and conservation agencies compared with the situation prior to the Second World War. In general, ornithology continues to combine professional scientists and spare time researchers in one optimal, synergistic group working at high scientific levels (Bairlein & Prinzinger 1999).

David Lack and the New Avian Biology in the United Kingdom (1942–1947)

From the 1920s to the early 1940s, the journal of the British Ornithologists' Union, *Ibis*, continued to publish mainly conventional papers on geographical ornithology consisting of expedition reports and detailed specimen lists, but hardly any biological articles. The New Avian Biology seemingly went unnoticed in Britain. Several British ornithologists, generally field ornithologists working outside the official ornithological establishment in the United Kingdom, had published important "biological" books and articles (mainly in the journal *British Birds* founded in 1907) on the lives of British birds since about 1900. This literature, however, remained on the fringes of British ornithology and had no influence on the editorial policy of the *Ibis*. Examples are several works by Edmund Selous (1901, 1905a,b) on the behavior of birds and on sexual selection; Eliot Howard (1907–14) on the behavior of warblers and on territory theory; Frederick Kirkman and his co-workers (Kirkman et al. 1910–13) on British birds; Eagle Clarke (1912) on bird migration; Julian Huxley (1914, 1922, 1925) on the courtship behavior of the Great Crested Grebe, Red-throated Diver/Loon, Pied Avocet, and other birds; Edgar Chance (1922, 1940) on the breeding habits of the Common Cuckoo; James Burckitt (1924–26) on an individually marked population of the European Robin, or Max Nicholson on *How birds live* (1927), *The study of birds* (1929), and *The art of bird-watching* (1931), and James Fisher's bestseller of 1941 *Watching Birds*. The biological significance of these studies was generally recognized in Britain only many years later (Lack 1959).

It is interesting to note that although most of these works were reviewed favorably and in detail in *Ibis*, the reviews did not lead to a change in the editorial policy of that journal or in the conservative attitude of the older generation of British ornithologists. William L. Sclater edited *Ibis* under the traditional policy from 1913 until 1930, followed by Claud B. Ticehurst until 1941. The latter also resisted suggestions to modernize the journal, but his successor Claude H.B. Grant nominated David Lack (1910–1973) as "Biological Assistant to the Editor" in 1942 in order to attract biological articles to *Ibis*.

As an undergraduate (in natural sciences) at Cambridge (1929–1933), Lack had watched birds in the surroundings of the city, discovering for instance double-brooding in the European Nightjar. He later pursued ecological and life-history studies of British birds during his spare time as a schoolmaster at Dartington Hall in Devon. His publications dealt with habitat selection (his term: Lack 1933) and with the territory theory (Lack & Lack 1933, with his father Lambert Lack). In 1937 he drew up a "Review of bird census work and bird population problems" in *Ibis*; his famous book *The life of the Robin* appeared in 1943. His papers of the 1930s, which included theoretical matter and interpretations, appeared in non-ornithological journals presumably because they would have been rejected by the editor of *Ibis*. In these papers Lack quoted from the German-language ornithological literature and was certainly aware of the modern biological contents of Stresemann's *Journal für Ornithologie*. He spent four months at the Senckenberg Museum in Frankfurt a. M. in 1929, having learned to speak German fluently (Lack 1973; Thorpe 1974).

In 1937, Huxley recommended to Lack an ecological study of the species differences and other aspects of the Galápagos finches in the field, and obtained funds for Lack's expedition to the islands from December 1938 until April 1939. Lack had met Ernst Mayr during a trip to the USA in 1935 and on his return journey from the Galápagos Islands stayed with him in New York for several weeks in 1939. Mayr tried to spread Stresemann's

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"gospel" in the United States, where he influenced some of the New York birders and encouraged Margaret Nice to write up her population study of the Song Sparrow, which he published as editor in two volumes of the *Transactions of the Linnaean Society of New York* (Nice 1937, 1943).

Discussions of Lack's expedition results (*Darwin's Finches*, Lack 1947) influenced Mayr's interpretations of bill-size differences in these finches. As he explained in his appreciation of Lack's work (1973: 433): "The emphasis in species studies during the 1930s and 1940s was strongly on the nature of isolating mechanisms and their origins. It was David Lack more than anyone else who restored balance by emphasizing the importance of ecological compatibility between species". It was Lack who brought ecology into the evolutionary synthesis, as Mayr (1947) remarked in his article on "Ecological factors in speciation".

Lack suggested publishing his Galápagos findings in the *Ibis*, "but received so discouraging a reply from the late editor [Ticehurst] (before he saw the paper), and at the same time so pressing an invitation from the CAS [California Academy of Sciences], that [he] accepted the latter" (Lack 1941: 637). Ticehurst had objected to explanations and interpretations if they ventured beyond the realm of fact-gathering, mostly faunistic lists (though to be fair to Ticehurst, the paper was also just over 150 pages long).

In a letter to Mayr, Lack confessed that the younger ornithologists in Britain "are all very disturbed about the state of the *Ibis*, but we are all too busy to do anything about it". In his reply Mayr wrote: "…If you can round up sufficient members who are dissatisfied and say so, you will not have any trouble instituting a new deal" (Johnson 2004). Lack adopted Mayr's suggestion to start a campaign for changes in British ornithology. He started to review in *Ibis* biological papers on birds published in a wide range of journals dealing with topics as diverse as physiology, genetics, and endocrinology (20 years after Stresemann had started a similar program in his *Ornithologische Monatsberichte*). By October 1945, when Lack was appointed Director of the Edward Grey Institute of Field Ornithology (EGI) at Oxford University, the "revolution" in the *Ibis* was well on its way, and was finally completed in 1947 when R.E. Moreau was made its editor. As Moreau (1959: 29, 33) later stated: "A revolutionary change occurred [in the late 1940s], as *Ibis* contributions came to reflect the fact that ornithology was no longer inbred and isolated from the main currents of biological science; ….. the *Ibis* was increasingly filled, up to three quarters, with biological papers".

It should be emphasized that these conceptual changes in British ornithology did not reflect a gradual and natural advance of a science into more complex biological fields of life history, behavior, and evolution after the systematic-faunistic basis of ornithology had been established. Rather, the "revolution" in the *Ibis* (from which modern British ornithology originated) occurred through the infiltration of a small group of young, biologically-minded ornithologists struggling against the conservative attitude of the majority of older colleagues. British ornithology "had needed a reorientation away from collecting, anatomy and classification to the study of living birds in their natural surroundings" (Johnson 2004: 544). As in Central Europe, this reorientation included a shift of centers of activity from the museums to zoological institutes at universities or to independent research organizations. Lack's research program at the EGI emphasized life history, evolutionary ecology, and population biology of birds, culminating in his classic of animal ecology *The Natural Regulation of Animal Numbers* (1954), where he placed ecological ideas in the context of natural selection. The EGI became a major training center for British ornithologists of the next generation. Up to the early 1990s, 130 doctorates were granted to students at the Institute (Johnson 2004: 545).

Lack's significant contributions during the 1960s and 1970s were presented in his well-known books *Population Studies of Birds* (1966), *Ecological Adaptations for Breeding in Birds* (1968), *Ecological Isolation in Birds* (1971), and *Island Biology, illustrated by the Land Birds of Jamaica* (1976). In this last work he postulated that "ecological impoverishment", rather than a decrease in immigration rate with distance, explains the decrease in species numbers on remote islands. He summarized his ideas on population regulation in birds as follows. The reproductive rate – evolved through natural selection – is that which results in the greatest number of surviving offspring per pair, and popuation density is regulated by density-dependent mortality, in most species by food shortage outside the breeding season. However research in recent decades has resulted in the discovery that the limitation of breeding density by territorial behavior is widespread among birds. Based on the evidence available to Lack at the time, he could not accept that territorial behavior limited density. He also greatly underestimated the importance of nest sites in limiting bird breeding densities. There is also experimental confirmation available now that the breeding densities of birds can be influenced by all the potential limiting factors, including food supply, nest sites, predators, parasites, and competitors (Bennett & Owens 2002, Newton 2003). See Haffer (2008) for more details.

These examples of the modernization of ornithology in the United Kingdom and in Central Europe illustrate two alternative modes or models of an ornithological paradigm shift: starting from the "periphery" of a national group progressing inward (centripitally, in the UK and North America), or starting from the professional center of a national group progressing outward (centrifugally, in Central Eu-

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rope). In both cases the modernization of ornithology was a "revolutionary" transformation occurring in a relatively short period of time through the influence of mainly one person or a small group of individuals, rather than through a slow and gradual transition and the influence of many people over a long period.

Ornithology became a unified and, at the same time highly diversified biological discipline only during the mid-20th century after having been subdivided into two widely separated branches – systematics and natural history – for over two centuries. Modern ornithologists thus returned to the broad holistic view of John Ray and other early masters (Haffer 2007a).

DISCUSSION

Conceptual and biographical histories of ornithology. There are basically two different ways of looking at the history of any science such as ornithology:

(1) A theoretical or conceptual history stresses the theoretical contributions, ideas, and interpretations in publications by ornithologists and follows the various research traditions over time, their conception and their results, and their final disappearance or amalgamation with other branches of research. We define a research tradition loosely as a research program that can be followed through time over more than one generation of researchers; the development of certain ideas or questions asked, or the direction taken by the investigation of important themes in time, like "exotic ornithology", "animal species and evolution", "breeding biology in general or as applied to a specific group of birds", "behavior of birds", etc. Biographical details of individual ornithologists in the past are reduced to a minimum in this approach to the science because they are judged to be hardly relevant. Such biographical information can, at best, serve to explain or better understand the success or failure of ornithologists.

(2) A biographical history of ornithology on the other hand emphasizes the lives of past ornithologists, and can, by restricting itself to the life of a single person or small group of people, occasionally lose sight of the significance of wider connections within the historical development of the field. Most of the important historical surveys of ornithology unite aspects of the conceptual and the biographical approaches by giving accounts of the theoretical contributions of earlier ornithologists as well as at least some information concerning their lives.

In this study we have stressed the theoretical achievements of the ornithologists covered but have neglected biographical detail. Obviously a most important factor for the success of important ornithologists is their personality type, but external circumstances can also make an enormous contribution to their career. Examples of this are John Ray in the 17th and Erwin Stresemann in the 20th century. Over many decades Ray received financial support from the family of his pupil and friend Francis Willughby – who died young – which enabled him, since he was unable for political reasons to practise as a clergyman, to write substantial works on plants, mammals, fish, and birds as well as natural history in general that considerably influenced the development of these fields. By contrast, Blasius Merrem recognized as early as the 1780s the necessity of combining systematics and field ornithology in a general ornithology, but fate denied him the opportunity of realizing his plan so that in 1788 only the introduction to his *magnum opus* appeared.

Facts and interpretations. Many early naturalists collected descriptive facts, e.g. on the geographical-ecological occurrence of birds, on their song, their breeding behavior, their molt, their diet, etc. Some researchers asked certain questions in order to establish a relationship between particular observations, thus allowing a scientific/biological interpretation or conclusion, e.g. the climbing ability and corresponding morphological adaptations in nuthatches and woodpeckers (C.L. Brehm), or the length of the autumnal migratory restlessness period in captive birds relative to the distance to their winter quarters (J.A. Naumann). In the 18th century, physico-theology provided an important theoretical framework and was a useful stimulus for naturalists to look for examples of directed design in the organic world, and hence to study the adaptations of birds in their structures, behavior (e.g. injury-feigning in ground-nesters), or plumage colors (e.g. protective coloration). Adam von Pernau, and even more so Pastor Zorn in the 18th century, as well as Faber, C.L. Brehm, and Gloger in the 19th, not only described many avian phenomena but also attempted to relate them to other features of avian life, and thus to interpret their biological significance and draw comparisons. Other ornithologists like Bechstein or J.F. Naumann hardly made any use of this scientific approach.

Stresemann (1926a: 227) recognized these points early in his analyses, but over-generalized when he stated that the ornithologists of the early and mid-19th century "still lacked intellectual leadership, the ability to ask the right questions, and a path into a comparative methodology. Ecology, sociology were unknown terms then and their observations were simply stated as facts without any attempt to relate them to each other – with certain outstanding exceptions, such as Faber's *Über das Leben der hochnordischen Vögel* [*On the life of birds in the far north*] (1825–1826)". Similar exceptions were also the works of A. von Pernau, J.H. Zorn, and J.A. Naumann.

Acknowledgments. At the start of our work was a rare copy of the little book on the *Vogelsteller* [*The Bird-Trapper*] (1789) by Johann Andreas Naumann, which J.H. received as a gift from Frau Amélie Koehler (Freiburg). Tim Birkhead (Sheffield), Hans

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Online Appendix 1
Species knowledge of some Central European ornithologists: 16th and 17th centuries
http://zoologicalbulletin.de/BzB_Volumes/BzM_59/Final%20Appendix%201.doc

Online Appendix 2
Species knowledge of some Central European ornithologists: 18th century
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Online Appendix 3
Species knowledge of some Central European ornithologists: 18th and 19th centuries
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Online Appendix 4
Modern German and English bird names
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Endnotes

[1] For the spelling of the name Gessner (with double 's') see Pyle (2000).

[2] '*Petino*' is a latinized form derived from the Greek *peteinós* (= feathered, winged) and *petomai* = I fly. Petino-theology is therefore *Winged-Theology* or *Ornitho-Theology*.

[3] Wenzel (1988: 99–100) quotes another long poem by Naumann, in which he described the very wet year of 1770.

[4] A discussion and critical summary of Bechstein's work on forest entomology is provided by Schwerdtfeger (1983).

[5] This is a reference to the works of C.K. Sprengel, who in the context of physico-theological work in the surroundings of Berlin had discovered the pollination of many plant species by insects, as well as their corresponding mutual adaptations.

[6] In this book Bechstein stated that the author's name had remained unknown to him. This was doubted by Schlencker (1982) because several ornithological authors in the late 18th century were well acquainted with Pernau's name (see e.g. von Göchhausen above), and he presumed that Bechstein had personal reasons for his assertion.

[7] When Bechstein discovered Collared Flycatcher in 1795 he called it *Muscicapa collaris*, a name that was preoccupied by an African species of the genus named by an earlier author. Therefore it was a later name for Collared Flycatcher (= *M. albicollis* Temminck, 1815) which became the valid one.

[8] Marsh Sandpiper does not occur in America, which is why Bechstein in his translation of Latham's *Synopsis* (1796) could not have referred to the species, as Pfauch (1989: 15) erroneously stated.

[9] Though Bechstein too established some simple causal connections, such as between neck length and the up-ending feeding habits of swans (Mauersberger 1990: 37).

[10] Taxa still currently valid are printed **bold**, valid complete species names are also **underlined**. The review of the Naumanns' names in von Boetticher (1957) is incomplete.

[11] See Dornbusch (2001, *Anhang* [Appendix] 3). Today there are still an adult and an immature specimen in the collection of the Naumann Museum, Köthen (G. Hildebrandt, pers. comm.).

[12] The many Latin names of these forms, which he published with his "*mihi*", are invalid synonyms.

[13] The term "species" has three separate meanings, which must be clearly distinguished from each other: (1) A particular species taxon, i.e. a particular bird species (e.g. Eurasian Robin or Golden Oriole). (2) The taxonomic category of species, between genus and subspecies, whose boundaries can be broadly drawn to include several geographical forms, or narrowly drawn to include only one or a few subspecies. (3) The theoretical concept of the species, i.e. what a species represents in general, (e.g.) a reproductive community (within the framework of typological or evolutionary biological thinking), an evolutionary lineage in geological time, or a constant type in the realm of organisms. See also Bock (1995).

[14] At present we have not been able to discover any taxonomic names introduced by Gloger which are no longer valid.

[15] "Providence" in the sense of the Christian teaching of a divine guidance of human fate.

[16] Since 1830 Professor Steffens had been a personal friend of the future King Friedrich Wilhelm IV. It was probably at Steffens's suggestion that Gloger wrote three extremely lengthy letters to the Prince in which he presented his ideas in a most verbose manner and petitioned him (in vain) for financial support (*Staatsarchiv*).

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