Kurzfassungen der Plenarvorträge

Adkins-Regan E

Hormones and the development of sex differences in behavior

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Birds are diverse in their degree of sexual dimorphism in behavior as well as morphology. Some are quite monomorphic behaviorally, while others have striking sex-specific behaviors such as male displays or vocalizations. Much attention has been paid to the evolutionary origins and selective pressures responsible for this diversity. A necessary complement to an understanding of the ultimate causes of dimorphism is the discovery of the proximate endocrine and other physiological mechanisms that lead to its development and adult expression. Experiments with Japanese Quail (*Coturnix japonica*), a precocial species with male-specific crowing and strutting, have shown that some of the sex differences are produced by hormonal dimorphism in adulthood (activational effects), whereas others are produced by permanent actions of sex steroids early in development, during the embryonic period (organizational effects). Experiments with Zebra Finches (*Taeniopygia guttata*), an altricial species, have revealed organizational effects on singing and mating that occur after hatching, during the nestling period. In both species, organizational effects are due primarily to estrogens, not androgens. The overall pattern of organization differs between the two species in interesting ways. Thus, early treatment with estrogen feminizes crowing in male quail but masculinizes singing in female Zebra Finches. Dimorphic behavior also includes mate preferences and choices, where the behavior itself is not necessarily dimorphic but the targets to which it is directed are. Experiments with both species suggest that sex differences motivating birds to mate or pair are produced by organizational rather than activational hormone actions. Zebra Finches are socially monogamous and form permanent pair bonds. Both sexes are motivated to pair, and pairing interest and success are expressed through monomorphic affiliative behavior such as clumping, mutual preening, and spending time in a nest together. Young juveniles direct this behavior toward family members. As they approach sexual maturity, the targets for the behavior shift from the family to potential pairing partners. What is the role of sex steroid hormones, if any, in adult pair bonding? Is it involved in the developmental shift in the target individuals for affiliative behavior? Although many species of birds form pair bonds, little is known about their physiological mechanisms. Experiments with adult Zebra Finches have shown that interfering with sex steroid actions has no effect on pairing interest or success in either males or females. Such a lack of significant involvement of sex hormones in adult pair formation may be widespread in other species that pair permanently, even when not actively breeding. Regulation of adult pairing by sex hormones is more likely to occur in species that pair seasonally, but even then indirect evidence suggests that high levels of sex steroids are not always necessary for continued maintenance of the pair relationship throughout the breeding season. The concept of hormonal organization, and the results of the experiments with Japanese Quail and Zebra Finches, raise a number of interesting questions, such as: (1) what other hormones and neurochemicals might be involved in mechanisms for pair bonding in continuously paired species, (2) what kinds of evolutionary changes in development have given rise to species differences in the degree of sexual dimorphism, and (3) what is the phylogeny of the major patterns of hormonal organization in birds? Supported by the National Science Foundation, U.S.A.

Blondel J

The story of Mediterranean Blue Tits: How to cope with heterogeneous and rapidly changing environments

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A basic problem in evolutionary biology concerns the adaptation of populations to environments that are heterogeneous and change rapidly. Mediterranean landscapes are highly dynamic ecological systems with mosaics of habitats that are dominated by either deciduous or evergreen trees, such as the patches of oakwoods with variable proportions of deciduous Downy Oak (*Quercus humilis*) or evergreen Holm oak (*Q. ilex*). The particular oak habitat type determines the timing of the leafing of trees in spring and, hence, the development of leaf-eating caterpillars which are the preferred prey of the Blue Tits (*Parus caeruleus*). The leaves of deciduous oaks develop one month earlier than those of evergreen oaks and, therefore, provide food for caterpillars one month earlier. Because 100% of the foliage of deciduous oak is renewed each year in contrast to only 30% of the foliage of evergreen oaks, the abundance of caterpillars is much lower in evergreen than deciduous forests. A large number of habitat types has been studied in two landscapes of southern France, one of which is on the mainland where deciduous oaks are more common and the other on the island of Corsica where evergreen oaks dominate. Combined with experimental approaches, these study sites provided a wealth of data on phenological, morphological, genetic, behavioral and physiological responses of Blue Tits to the various habitat-specific features and constraints of the environments. The one-month difference in the phenology of oaks and associated invertebrates results in a corresponding one-month difference in the onset of breeding for those populations that best match the supply/demand ratio of food. Populations that settle in the less common oak forest in each landscape and miss the peak of food production, however, have much lower breeding success and produce fewer offspring of poorer quality. This local maladaptation was shown by minisatellite markers to result from gene swamping from rich to poor habitat patches, producing a source-sink population structure. Blue Tits breeding in the productive deciduous oak habitat patches start to breed earlier, lay more eggs, and produce more offspring of better quality than those that settle in evergreen oakwoods. They are also larger and heavier but cross-fostering experiments have shown that differences in environmental constraints result in adaptive differences in nestling growth and hematocrit values leading to environmentally-induced phenotypic plasticity. In evergreen oak habitats, various combinations of constraints, such as food shortage, parasite loads and high temperatures, create more variable and sometimes extremely poor breeding conditions for these late breeding birds. Parasites are especially harmful when food is scarce, and may reduce the heritability of size-related traits, thus limiting evolutionary responses to selection. Missing the peak of food production can be very costly and may have severe consequences on fitness and survival: doubly-labeled water experiments have shown that the metabolic effort of adults rearing chicks increases steeply as the time difference between breeding date and peak caterpillar productivity increases, which forces adults to work far beyond their sustainable limits. Radiotracking showed that parent tits in the poor evergreen habitats forage at much greater distances from their nest, but that the amount of food delivered to each chick is similar to that in deciduous oakwoods due to smaller number of chicks and a greater mean prey size. Foraging distances and searching time are longer for mismatched adults, with severe consequences for survival prospects. Inter-habitat phenotypic variation in life history traits is considerably higher on Corsica than on the mainland, providing a striking example of an adaptive response of suites of life history traits to habitat-specific selection regimes that operate on a scale that is much smaller than the scale of dispersal and potential gene flow. This difference between mainland and insular patterns is due to reduced dispersal in the island birds, which is part of the insular syndrome. Interestingly, weak genetic differentiation contrasted with large phenotypic variation in the populations on Corsica. Despite significant heritability of and selection for several traits, no significant change was found over time. A variety of factors may explain why traits may have considerable additive genetic variance and appear to be under directional selection and yet do not evolve. The study system illustrates an extreme case of habitat heterogeneity and divergent selection regimes at landscape scale for small passerines in temperate habitats. The most fascinating aspects of the story, with a cascade of consequences for life history, is the one-month difference in breeding time between populations, depending on the morphotype of oakwood chosen for breeding. Several experiments in the field and in aviaries have been devised to determine whether variation in their traits is a plastic phenotypic response or has resulted from genetic differentiation in response to local selection regimes. The observed variation in Mediterranean Blue Tits illustrates a large body of theoretical work, and supports the divergence-with-gene-flow model of speciation, whereby reproductive isolation can evolve between populations that are connected by gene flow whenever divergent selection is strong relative to gene flow. Wherever habitat heterogeneity is a mixture of very different habitat patches, the resulting reaction norm includes either local specialization, phenotypic plasticity, or local maladaptation depending on the size of the habitat patches relative to the average dispersal range of the organism.

du Plessis MA

Delayed dispersal and cooperative breeding in birds

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Cooperative breeding, a reproductive system in which more than a pair of individuals behave parentally towards young in a single nest or brood, has attracted significant attention over the past four decades. By the early nineties, signs of agreement among workers in the field seemed to draw the earlier excitement in the field to a close. More recently, however, several new lines of argument have reinvigorated the field, not the least of which have been the debates centered on the role of its evolution on ecology, life history and phylogeny. In order to understand the evolutionary basis of cooperative breeding, a framework involving the dissociation of two key questions has generally been used. First, why do birds delay dispersal, and second, given delayed dispersal, why do the large majority of philopatric birds provide care to offspring on the territory in which they live? I propose to focus largely on the first question, but with cursory reference to some of the current thinking on the second. As reproductive maturity is reached, an individual is faced with the decision to breed independently or delay breeding. In the latter case, there are three options: delay breeding by staying on the natal territory either as a helper or as a non-helper, or to leave the natal territory as a "floater". If the cost and likelihood of successful breeding vary spatially and temporally, individuals may delay dispersal and/or independent breeding in response to the following: the quality of the territory, the depressibility of key resources, the risks associated with dispersal, and/or, in unpredictably variable environments, the seasonal variation in territory quality. The dispersal threshold model suggests that delayed reproduction may in some instances ultimately yield higher lifetime reproductive success than breeding independently in territories of poor quality. Various constraints and opportunities affect our attempts to understand the relative importance of the above factors. First, measures of territory quality have been fraught with complications and generally the best that can be done is to control indirectly for their effects in demographic analyses. Secondly, when breeders allow offspring to remain on the parental territory, there is potential for competitive conflict for access to critical resources on the territory. It is therefore important to consider the nature of the critical resources in terms of their depressibility. Thirdly, it is difficult to quantify the risks associated with dispersal accurately. In this connection, some colonial species breed in circumstances where most individuals in the colony have access to nest sites and experience similar environmental conditions. Thus, colonial birds are not necessarily exposed to the risks commonly associated with dispersal, which has been suggested to have a strong influence on the reproductive decisions that territorial cooperatively breeding birds take. Fourthly, in unpredictable environments, the severity of environmental conditions during different breeding seasons vary greatly. This presents some non-breeders with the opportunity to base their reproductive strategies on seasonal variation in territory quality. While it is possible to identify constraints operating on individual cooperative breeders or to agree on shared life-history characteristics, it still cannot be predicted when species will adopt the strategy of staying at home or to float non-territorially as non-breeders. The absence of strong predictive capacity to explain the phenomenon of delayed dispersal is of concern, particularly given that similar ecological and life-history features are shared by a large majority of species that do not delay dispersal and/or breed cooperatively. A potentially fruitful approach could lie in the study of delayed dispersal and cooperative breeding among irregular cooperative breeders or those species that show extensive variability in degree of sociality.

Edwards S

Genomics and ornithology

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Like many areas in ornithology and ecology, new technological advances have allowed the avian genome to come into sharper focus. The recently completed draft chicken genome sequence is but a start. New initiatives, including complete sequencing of the Zebra Finch (*Taenopygia guttata*) genome, will accelerate the development of a truly comparative genomics of birds. We can already glimpse this comparative genomics through the few available multi-kilobase aligned nuclear genome comparisons among birds, chromosome painting studies, and also through large-scale bioinformatics analyses of avian and reptilian genomic DNA. These studies suggest that avian genomes will be very conserved in terms of their overall organization, synteny (order) of genes along the chromosome, genome content and rate of evolution, and may exhibit specific rules, such as a faster rate of sequence evolution on autosomes and on microchromosomes. But genomics has much more to offer ornithology than comparative genomics and phylogenetics. New studies employing macro-and micro- array analyses of expressed genes have begun to suggest, in broad outline, networks of ecologically relevant genes that help birds combat pathogens and whose regulation may undergo bouts of evolution during epizootic events. Such micro-array platforms may provide an avenue for examining gene expression differences in a variety of ecological contexts - between dominant and subordinate individuals, breeders and migrants in low- and high- quality habitats, and between phenotypically plastic behavioral and hormonal syndromes in social systems such as cooperative breeding. Large-scale expressed sequence tag (EST) surveys of brain transcripts in the Zebra Finches promise to provide resource for examining changes in brain structure and function during ontogeny and in response to song. Ultimately, with the advent of the first comparative maps of avian genomes, genomics will shine a bright light on the process of speciation itself. Avian genomics is still clearly in its infancy, and the challenge for an integrated ornithological genomics is to marry the considerable technical challenges of scaling up in our surveys of genomic variation with field studies of variation in behavior, ecology and physiology. Such cross-disciplinary efforts will help pinpoint those regions of the genome participating in adaptive change, and help predict phenotypic changes resulting from changes in DNA.

Greenwood JJD

Citizens, science and bird conservation

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Collaborative work by amateurs has made substantial contributions to ornithology and to bird conservation science, at least in some countries. In those countries, it has expanded the numbers of citizens who are well-informed and rationally concerned about environmental issues. Yet there is potentially much more that could be done, in terms of the topics investigated, the countries involved, and the numbers of people participating.

Jarvis ED

Learned birdsong and the neurobiology of human language

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In this plenary lecture, I will present insight that my colleagues and I are gaining from the study of vocal learning brain systems in birds into the neurobiology of language in humans. Gaining such insight required a multidisciplinary approach that includes, but is not limited to, the use of behavioral molecular mapping tools to functionally map brain areas involved in learned vocal communication, and a comparative approach that broke down old misconceptions of differences between avian and mammalian brains. The hypothesis that emerged is that distantly related vocal learning birds (songbirds, parrots, and hummingbirds) and humans each appear to have evolved similar, although not identical, specialized forebrain pathways: one involved in the production of learned vocalizations and the other involved in their acquisition, including that of syntax. These vocal learning pathways appear to have evolved out of a preexisting motor brain system that, I argue, predates the ancient split from the common ancestor of birds and mammals. Although the hypothesis will require the development of novel technologies to be fully tested, the existing evidence suggest that there are strong genetic constraints on how vocal learning brain systems can evolve.

Merton DV

The Kakapo: some highlights and lessons from five decades of applied conservation

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The Kakapo (*Strigops habroptilus*) is a giant, flightless, nocturnal parrot endemic to New Zealand, in the monotypic subfamily Strigopinae. It is the largest parrot, adults weighing <4.0 kg. The kakapo has combinations of features not shared by any other bird and is unique amongst parrots in having a "lek" mating system. Its origin and relationships with other parrots are obscure and distant, and it is one of the last surviving members of a unique avian-herbivore/plant system that disappeared with the extinction of the moas. The Kakapo was well-adapted to ground mammal-free conditions in prehistoric New Zealand, but proved pathetically vulnerable to predation by introduced mammalian carnivores. By the 1990s it had declined to extinction throughout its natural range and was critically endangered. It survives today on three off-shore islands to which it was relocated in 1975 for its protection. Attempts to avert its extinction were first made in the late 1890s when the New Zealand government transferred ~375 birds to islands in Dusky Sound, Fiordland. Stoats reached the islands soon after, and the venture failed. Fifty years were to elapse before a further conservation attempt was made. In the late 1950s and 1960s, ~10 birds were located within Fiordland's Milford catchment and an attempt was made to establish a captive population. All nevertheless proved to be male, and most died within a few months. A third attempt to save the species was launched in 1974 and continues to the present time. Using a range of “close-order management” techniques on free-living birds, effort is now directed at maximizing survival of naturally produced eggs and young, increasing breeding frequency and managing genetic diversity in order to improve low fertility and hatchability. Techniques include manipulation of the breeding population to optimize genetic diversity; inter-island transfer of breeding stock in order to capitalise on locally abundant foods that trigger breeding because Kakapo breed at two to five yearly intervals in synchrony with unusually heavy fruiting or seeding of certain native plants; support of breeding females through supplementary feeding; manipulation of female pre-breeding weights to increase the proportion of female young produced; artificial insemination to increase fertility and improve genetic representation; physical protection of nests; and intensive monitoring of nests throughout breeding coupled with intervention as necessary. A great deal has been learned during the course of the program – much of it relevant to other rescue and recovery programs. Since 1995, Kakapo numbers have increased by 68%; the global population now stands at 86 individuals.

Piersma T

Using the power of comparison to explain habitat use and migration strategies of waders worldwide

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Waders, or shorebirds, form an ecologically homogenous group of birds that, despite the homogeneity, show clear correlated contrasts in habitat use and migration distance between closely related species pairs. Within species, moreover, there is often distinct variation in breeding and wintering latitudes, that is, migration distance. I review such contrasts at different taxonomic levels, and evaluate what can be learnt from them about selective forces acting on habitat selection and the evolution of migration strategies in birds. The worldwide migration system of Red Knots (*Calidris canutus*) is one example. These sandpipers breed only on high arctic tundra but move south from their disjunct, circumpolar breeding areas to nonbreeding sites on the coasts of all continents except Antarctica, between latitudes 58° N and 53° S. Due to their specialized sensory capabilities, Red Knots generally eat hard-shelled prey found on intertidal, mostly soft, substrates. As a consequence, ecologically suitable coastal sites are few and far between, so they must routinely undertake flights of many thousands of kilometres. In contrast to predictions based on the low costs of living and thus the freedom to allocate nutrients to fuel storage, Red Knots at tropical intertidal sites have lower fuelling rates than birds at more southern or northern latitudes. This leads to more constrained annual schedules in the south temperate and tropical wintering populations. Whether this affects overall mortality rates or seasonal mortality patterns, with concomitant differences in selective regimes, will be discussed on the basis of new comparative demographic studies on Red Knots and Bar-tailed Godwits wintering at different latitudes.

Wanless S

Climate change and north-east Atlantic seabirds

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The coastal shelf seas around the north-east Atlantic are some of the most productive regions in the world. They are already at risk from a range of anthropogenic pressures, such as overfishing, development of wind and tidal energy schemes, and pollution; and the situation is currently being exacerbated by marked and rapid changes due to global warming. Seabirds are charismatic top predators

in these systems, and are being caught increasingly in the crossfire between human exploitation and climate change. In conjunction with information on ocean climate, long-term data on seabird demography, phenology and diet are being used to predict the consequences of current and future climate change on seabird populations and to interpret the interspecific and regional differences that are apparent. These population level data are being complemented by detailed studies of individuals, using novel technology, that aim to identify important foraging areas and quantify foraging performance under a range of environmental conditions. I provide an overview of the current situation and highlight the species and regions that are most at risk.

Wiltschko W

Magnetoreception in birds: Two receptors for two different tasks

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The geomagnetic field is a reliable, omnipresent source of information for orientation: its vector provides directional information and can be used as a compass; and the spatial distribution of its intensity and/or inclination, with gradients running from the magnetic poles to the magnetic equator, can provide information on position as a component of the navigational "map". Furthermore, special magnetic conditions can indicate specific locations, where they may act as "triggers", eliciting specific responses. Behavioral evidence indicates that birds indeed use the geomagnetic field for all these purposes. For magneto-reception, two hypotheses are currently under consideration. The "magnetite-hypothesis" assumes receptors that are based on magnetic particles, as described from the upper beak and ectethmoid region in birds. The "radical-pair model" proposes magneto-reception based on the modification of chemical processes in photopigments in the eye, where the modifications depend on the alignment of pigment molecules in the ambient magnetic field. Behavioral tests with migratory birds provide evidence for both hypotheses. For the first, a short, strong magnetic pulse designed to affect magnetite particles led to a marked change in the prefered directions, thus indicating the involvement of magnetite-based receptors. At the same time, tests showed that birds require light from the blue-to-green part of the spectrum for migratory orientation, and that this orientation can be disrupted by HF-fields in the MHz-range, indicating the involvement of photopigments and a radical-pair mechanism. The test-design of the various studies and the specific responses of the birds, as well as electrophysiological studies, suggest that light-dependent radical-pair processes in the right eye mediate directional information for compass use, whereas magnetite-based mechanisms in the beak provide information on magnetic intensity used in the navigational "map" and for the "trigger" functions.

Übersichtsvorträge beim "Deutschen Abend" (Montag, 14.08.)

Bezzel E

Birds in Germany: Some insights after nearly two centuries of comprehensive bird recording by birdwatchers and ornithologists

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The breeding bird fauna of Germany forms a representative sample of the bird fauna of the temperate zone of the western palearctic region. According to atlases of breeding birds at the end of the 20th century, the breeding ranges of species in Germany match those in surrounding areas. Germany has no endemic species. Of species found on more grid units than expected, those of forest and farmland dominate; and those that are sparser and rarer are birds of oligotrophic open land and wetlands. The present differences in the ranges of species between Germany and adjacent parts of Europe seem to be determined more by available habitat than by zoogeographic gradients. Population sizes vary similarly. According to data in the BirdLife/EBCC European Bird Database, those breeding species that are abundant in Germany are similarly abundant in adjacent countries as well. Only several very rare species show different patterns; but there is no species that is rare in continental Europe yet common in Germany. In the middle of the 19th century, the well-known German ornithologist Johann Friedrich Naumann published a detailed review in which he bewails the decline of birds in central Germany. As a result of fifty years of birdwatching and experience in professional bird trapping for food, he saw "modern" practices of increased farming and human persecution as the main causes for alarming decreases. Thirty years later, Karl Theodor Liebe published a list, according to which more species had declined than increased in Thuringia, particularly the larger non-passerines, due mainly to human exploitation of forests and open land. So there is a reliable history of the German bird fauna from before the Industrial Revolution in the second half of the 19th century, an event that marks the beginning of the change which has affected so many bird habitats up to the present. Detailed local and regional bird reports have existed since that time, giving insight into the dynamics of species diversity in central Europe. More than a hundred years ago, the relative number of records indicating negative trends or extinction in local or regional populations per time unit seem to have been higher than during the 20th century. In the 20th century, rather more regional species seem to have increased than declined. This may be due to prior preoccupation with recording species that were declining or disappearing locally; but it is surely also a result of successful efforts in protecting threatened and rare species nowadays. For some of the larger areas of Germany, published data and documented birdwatching over periods of differing socio-economic and technical conditions enable reconstruction of the number of species breeding annually over a long period through the 20th century. In Bavaria, the number of species breeding annually has increased by seven percent over the last hundred years, and the number breeding per decade by eight percent. This small but nevertheless surprising increase is contradictory to the findings of some local studies, and has to be interpreted carefully because the present situation may be masked by several influences. The increase is unlikely to reflect more bird recording activity in recent decades, but may well result from conservation efforts. Though the balance between new and lost breeders is positive over the last hundred years, it has still fallen in the last three decades. The number of introduced species increased from less than one percent in the first decade of the 20th century to nearly eight percent in the last. Moreover, the balance between new and lost species is related to the size of the area involved indicating a species-area relationship. The decline in common and widespread species within the last decades has involved populations in smaller rather than larger areas. Thus in Bavaria, where the overall trend per decade is positive, turnover in species in smaller areas tends to be negative: species diversity reacts more

sensitively at local than regional scales. A hundred years ago, birdwatchers and ornithologists in Germany focused on describing the situation rather than documenting the dynamics. So a huge amount of collected data was often published in detailed reports or lists. These irreplaceable historical sources not only provide information on the distribution of species but also such seasonal events as the arrival or departure of well-known migrants. The first seasonal records of migrants at the beginning of the 20th century compared with data collected a hundred years later indicate considerable changes in migratory behavior in some species.

Haffer J

The development of ornithology in central Europe

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The first genuine ornithologist in Europe since Aristotle was the emperor Friedrich II of Hohenstaufen whose work on falconry, written before 1248, includes a general account of birds based largely on his personal observations. Other medieval workers on birds were Albertus Magnus, Thomas di Cantimpré and Konrad von Megenberg. Gilbertus Longolius (1544) and William Turner (1544) reported on some birds of the Rhine region. The Renaissance encyclopedist, Conrad Gesner (1555), compiled the total knowledge of European birds at the time, listing 182 species in alphabetical order. The first local vertebrate fauna was published by Caspar Schwenckfeld (1603) who included brief accounts of c. 150 species of birds. Several collections of unpublished bird paintings from the late 16th and the 17th centuries also represent valuable faunistic records. Two separate research traditions in Europe originated around 1700 from the work of John Ray (1627 to 1705) in England: research into the systematics of birds, and research into the field natural history of birds. The principal early representatives of the natural history tradition in Germany were Ferdinand Adam von Pernau and Johann H. Zorn who published the results of their important field studies during the first half of the 18th century. They worked under the concepts of physico-theology employing the teleological principle, and were the first truly significant researchers of the biology of European birds. The first German bird book with excellent folio color plates was that of Johann L. Frisch which appeared in 1733 to 1763. Around 1800, two detailed handbooks on the birds of Germany were published by J. M. Bechstein and by J. A. Naumann, respectively. The text of Bechstein is more extensive than that of Naumann, but the color plates in the latter, prepared by his son Johann Friedrich, are superior. The Golden Age of central European ornithology from 1820 to 1850 saw the appearance of the splendid works of Johann Friedrich Naumann, Christian Ludwig Brehm, and Friedrich Faber who established a sound basis for the study of birds in this region and beyond. During the second half of the 19th century, many European researchers turned their attention to exotic ornithology, because large bird collections were arriving in Europe then from many different parts of the world. During those decades, the study of central European birds made little progress, despite a major controversy over instinctive versus purposive behavior in birds which did not stimulate any field research. The influence of the Darwinian theory of evolution (1859) had little impact among central European ornithologists until the end of the 19th century. From the 1920s onward, central European ornithology changed rapidly, and general biological studies began to take precedence over earlier systematic-faunistic work: the Stresemann revolution. This paradigm change had a worldwide impact, and it was soon recognized that the bird is a well-suited subject for studies into the problems of functional morphology, physiology, behavior and orientation in animals.