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## Introduction to plenary papers

A central feature of the scientific programs of international ornithological congresses is a series of plenary lectures, which include the Presidential Address. The 2nd Congress in 1890 in Budapest contained several major addresses by well-known ornithologists such as J. A. Palmén, A. Newton, R. B. Sharpe and M. Fürbringer. The tradition of the Presidential Address began at the 4th Congress in London in 1905 when R. Bowdler Sharpe presented a detailed history of the bird collections in the British Museum. From that time, all ornithological congresses have begun with the Presidential Address immediately following the Opening Session, the Beijing Congress being the one exception because Professor Bock had lost part of his voice due to a paralyzed left vocal chord (resulting from an operation at the end of April, 2002; he can talk normally now); his written address is included herein.

It has been a tradition for plenary lectures to provide overviews of major advances in the research fields of the lecturers chosen: Heinroth on the ethology of ducks and Lucanus on avian physiology at the 5th Congress; Lambrecht on avian paleornithology and Dunker on avian genetics at the 7th; Meise reviewing progress in systematics and Nice on the life history of the Song Sparrow at the 8th; and Mayr on avian speciation, Dorst on migration, Tinbergen on behavior and Lack on ecology at the 10th. Presidential addresses, in addition, sometimes reviewed historical aspects of ornithology, such as the contribution of amateurs in biology, the role of museum development and, as at the 23rd Congress, histories of the international ornithological congresses themselves.

Most plenary lectures have been published in the Proceedings of congresses, together with presidential addresses, and for the 1994 and 1998 congresses also separately as an issue of a major international journal to increase circulation. So we are pleased that the plenary lectures from the 23rd Ornithological Congress in Beijing, 2002, will be published in a separate issue of *Acta Zoologica Sinica*. Unfortu-

nately, one lecturer at Beijing, Roberto Cavalcanti (Brazil, Bird Conservation in South America), did not provide a manuscript of his talk. Henri Weimerskirch's paper on seabird ecology was submitted too late and just as an enlarged abstract. Due to the editorial policy of *Acta Zoologica Sinica*, it will now be published among the general records of the Proceedings, together with the RTDs and symposia. The other papers provide a diverse picture of current research topics in avian biology.

An additional plenary event was held for the first time at the Beijing Congress: a Presidential Debate. Two eminent protagonists were asked to present their cases for opposing views on an important topic in avian biology, in this case the origin of birds from reptilian ancestors. The two papers, from Larry D. Martin (An early archosaurian origin for birds) and Paul Sereno (Birds as dinosaurs), provide divergent interpretations on the evolutionary origin of birds, together with a wealth of citations from this vast literature. While neither author may convince a majority of ornithologists, we feel that these two presentations will provide much material for further thought on what is a core issue in avian biology.

We wish to thank all of the plenary speakers for their efforts in contributing to this volume, as well as the members of the Chinese Local Committee and the editors of *Acta Zoologica Sinica* for their assistance in organizing the Congress and publishing this volume. And through it we trust that all readers will discover many new and fascinating aspects of biology in the discipline that binds us together, ornithology.

Walter J. Bock,

President

23rd International Ornithological Congress

Special Editor, Plenary Lectures, Proceedings of the  
23rd International Ornithological Congress

Richard Schodde,

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## Presidential address: three centuries of international ornithology

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**Abstract** Science is always claimed to be international; and perhaps the best way to achieve that goal is through international meetings in which individuals attending have the opportunity to meet many others. But international congresses in science were slow in starting, and the 1st International Ornithological Congress in 1884 was one of the earliest of them. Fittingly, this Congress started because of a problem in avian biology that was in itself without borders, namely avian migration. One of the most fascinating aspects of avian biology is the annual north/south movement of many species of birds, about which little was known in the late 19th century. In multi-country Europe, the study of avian migration obviously had to be an international effort. Rudolf Blasius and Gustav von Hayek developed a grand plan for a multi-nation program on avian migration in Europe, obtained the support of Crown Prince Rudolf of Austria-Hungary, and announced the 1st International Congress of Ornithology in Vienna, April 1884 which was dedicated largely to migration studies. An elaborate scheme was established to collect and publish migration data from Europe which subsequently collapsed under a great mass of unanalyzed data in the 1890s.

The 2nd Congress in Budapest in 1891 was also devoted largely to avian migration, but had expanded to other areas of avian biology such as a major summary of avian classification contributed by R. B. Sharpe. The 3rd Congress in Paris in 1900 covered the gamut of ornithological research, its scope followed in London, 1905 and Berlin, 1910, where the next congress, set for Sarajevo, Yugoslavia, in 1915, became prophetic for the oncoming First World War. E. Hartert was largely responsible for re-establishing the congress in Copenhagen in 1926, with future ones set at every four years. The *Règlement des Congrès Ornithologiques Internationaux*, adopted in 1932, was only published at the Rouen Congress, 1938, formalizing the operation of the International Ornithological Committee. World events again interfered with the 1942 Congress scheduled for the USA, and the next congress to be held was in Uppsala in 1950.

The first non-European congress was held at Ithaca, New York, in 1962, and the first for the southern hemisphere was in Canberra in 1974. Modern congresses started with Berlin, 1978 where Donald Farner established the first International Scientific Program Committee, and formulated a new organizational Statutes and By-laws to replace the *Règlement*. A pattern of plenary lectures, symposia, contributed papers and round table discussions was established there too. By 1986 it became clear that the tasks of the Secretary-General had become too great for one person, and that more organizational continuity was needed in the IOC, leading to the creation of the position of a Permanent Secretary at the Ottawa Congress.

Ornithological congresses have continued to increase in size and complexity, and most importantly in cost to members, making it difficult for many interested ornithologists to attend. So the future of such congresses as a primary means of international contact among ornithologists is no longer entirely clear, and much effort needs to go into solving major organizational and programming problems so that ornithologists can look forward to another century of these valuable and pleasant meetings [*Acta Zoologica Sinica* 50 (6): 880–912, 2004].

## 主席致辞：国际鸟类学的三个世纪

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**摘 要** 科学需要国际交流, 国际会议也许是国际交流和认识其他同行的最好方法。然而, 国际科学会议起步较晚, 于 1884 年举办的第一届国际鸟类学大会即是最早的国际科学会议之一。召开那次国际会议的起因是探讨鸟类生物学中一个超越国界的自然现象, 即鸟类的迁徙。许多鸟类每年一次的南北迁移运动是鸟类生物学中最具魅力的问题之一, 但 19 世纪的人们对鸟类的迁徙了解甚少。在多国组成的欧洲, 如果研究鸟类迁徙则必须进行国际合作。Rudolf Blasius 和 Gustav von Hayek 制定了一个欧洲多国合作研究鸟类迁徙的宏伟计划, 并得到了匈牙利–奥地利王储的支持。与此同时, 二人发表了一项公告: 于 1884 年 4 月在维也纳召开第一届世界鸟类学大会, 会议主题是鸟类迁徙。会议制定了详细的收集和出版鸟类迁徙资料的方案。在 19 世纪 90 年代, 由于大量

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的数据没有分析,因而这项计划被迫终止。

第二届世界鸟类学大会于 1891 年在布达佩斯举行。会议的主题仍然是鸟类迁徙,但增加了鸟类生物学中其它方面的议题,包括对 R. B. Sharpe 鸟类分类系统的总结。第三届世界鸟类学大会于 1900 年在巴黎举行,会议内容涉及到鸟类学研究的各个领域,随后,世界鸟类学大会于 1905 年在伦敦举行,于 1910 年在柏林举行。在第一次世界大战前夕,于 1915 年在南斯拉夫的萨拉热窝举行了第六届世界鸟类学大会。第一次世界大战后,在 E. Hartert 的积极倡导和努力下,世界鸟类学大会于 1926 年在哥本哈根再次组建,提议将来每四年举行一次世界鸟类学大会。“国际鸟类学会议准则”于 1932 年被采纳,并在里昂会议上公布,1938 年世界鸟类学大会执行委员会正式成立。然而,世界大战再次干扰了计划于 1942 年在美国和 1950 年在乌普萨拉召开的世界鸟类学大会。

第一次欧洲以外区域的世界鸟类学大会于 1962 年在纽约的伊萨卡举行,1974 年首次在南半球的堪培拉举行世界鸟类学大会。现代世界鸟类学大会始于 1978 年的柏林会议,在这次会议上,Donald Farner 建立了第一个国际科学会议程序委员会,拟定了新的组织原则,运用议事程序代替了 *Règlement*; 并在这次会议上规定了全体会议、座谈会、会议论文和分组讨论等模式化会议程序。在 1986 年的渥太华世界鸟类学大会上,组委会意识到大会秘书长的任务量太大,另外大会需要更多的组织性和连贯性,因此大会开始聘任专职秘书。

世界鸟类学大会规模和复杂性不断增加,特别是与会人员的费用也与日俱增,这使一些鸟类学家难以参加会议。因此,将来国际会议是否是鸟类学家交流的基本方式不再十分明了,我们需要投入更大的努力去解决组织和程序问题,使鸟类学家们在另一个世纪期待到既有价值又令人愉快的国际会议 [动物学报 50 (6): 880 - 912, 2004]。

## 1 Introduction

Although the 21st century has just begun, now the third for International Ornithological Congresses, the history of the activities of those congresses since their founding in 1884 has been fragmentary. Erwin Stresemann (1938), in his presidential address to the 8th Congress, presented a history of what had happened before and provided some brief comments on the founding actions. But there has been almost no further discussion; and such analyses are difficult because of the absence of archival material and problems in obtaining complete sets of congress proceedings. Even when all proceedings are collated, a historical review is difficult because of a frequent lack of comments on decisions reached in official reports. As I progressed with the analysis and drafting of this history, it became ever clearer that much needed information in published proceedings was often inadequate, if not missing altogether. So considerable ‘reading-between-the-lines’ was required in putting together this account, as well as the recall of personal memories back to the 13th Congress in 1962.

The lack of a history of the international ornithological congresses has been most unfortunate because they are one of the earliest of world-wide international scientific meetings still operative. In this review, I will deal essentially with the history of the congresses themselves, without paying much attention to details of presented papers and the trends generated. After careful consideration, I chose to present this history congress by congress, despite the dullness from necessary repetition. Congresses are known by the name of

the city in which they are held; hence the 1974 Congress is the 16th or Canberra Congress, not the Australian Congress. A list of the congresses, the major officers, and citations to the proceedings is added in an appendix. The abbreviation IOC is properly used, as here, for the International Ornithological Committee, not for the International Ornithological Congress. In recent years some workers have gotten around this confusion by using the terms IOCommittee and IOCongress.

In the mid-1980's an archive was established for the papers of the International Ornithological Committee, its congresses, and its standing committees at the Smithsonian Archives of the Smithsonian Institution, Washington, D. C., USA. Although the existence of the IOC archive has been published in the reports of several successive congresses, wherein congress members have been urged to deposit papers relating to their work at different congresses, few such papers have been deposited. Most archivists and historians of science argue that it is best to keep all of the papers of a person together in a single archive which makes it most difficult to gather the papers of an organization such as the IOC and its congresses into a single location. Consequently, the papers of past congress Presidents and Secretaries-General, if available, have been scattered in archives all over the world. No attempt has yet been made to locate such papers, so that at this time it is impossible to know, in any comprehensive way, what materials are available on which to analyze the history of the IOC and its congresses. I strongly urge members of past and future congresses to either deposit their papers in the

IOC archives, or to inform the person responsible for the IOC Archive at the Smithsonian Institute of the location of the papers of congress officers and members. Ornithologists should consult Gephardt (1964 and supplements) for information on many of the central European ornithologists, now little known to present-day workers.

I will not comment here on the Ladies' (= accompanying member) Program and very little on congress excursions. Both have been standard components of all congresses ever since the 2nd Congress in Budapest. Moreover, I will omit discussion of most of the resolutions passed by the congresses.

## 2 The beginning—the 1st Congress, Vienna, 7–11 May 1884

Of all groups of organisms, birds are special in that a large number of species migrate annually between their breeding and non-breeding areas. Only a few other animals, such as whales, pinnipeds, some bats and a few insects (such as the Monarch Butterfly of North America) make such movements as part of their life cycle. Migratory birds are especially characteristic of those regions where modern ornithology developed; and early in the second half of the 19th century a number of ornithologists in Europe and North America turned their attention to this central aspect in the life of birds. At this time inquiries centered on the migration routes of species, such as whether the spring and autumn routes were the same (see Stresemann, 1951; 1975: 332–338). Work progressed much faster in North America (Rowan, 1933) because most of the work could be accomplished in the United States under the auspices of US federal agencies and the newly established American Ornithologists' Union. In Europe the problem was far more difficult because of a complex geomorphology and the diversity of countries in which recordings had to be made; more than individual cooperation was required. This led to the formation, in 1875, of an overseeing committee in Germany, followed in 1877 by similar ones in the United Kingdom and Austria-Hungary (Stresemann, 1975).

Out of this, Rudolf Blasius (Brunswick) and Gustav von Hayek (Vienna) conceived a grander scheme for organizing broad international cooperation in migration studies, and pushed for an international meeting to discuss it. Crown Prince Rudolf of the Austro-Hungarian Empire (who was fascinated with ornithology and hunting since childhood) approved the plan which led to the announcement of the first International Ornithological Congress in Vienna in April 1884. Prince Rudolf was the patron of the 1st Congress. This meeting was predominantly a European one; ornithologists mainly from Austria and

Germany attended, with only a scattering from other European countries, and none from Hungary, the United Kingdom or North America. Fortunately this first international meeting of about 150 delegates was called the “International Ornithological Congress” and not the “European Ornithological Congress”, even though that is what it really was; hence our birth date is 7 April 1884. The International Ornithological Congress was the first such meeting in the biological sciences (and possibly all sciences), and preceded the first International Zoological Congress (1889) by 5 years and first International Entomological Congress (1910) by 26 years. At the opening of the 1st Congress, Dr. Gustav F. R. Radde (Tbilisi [= Tiflis], Georgia) was elected President, and Dr. Gustav von Hayek (Vienna) Secretary. A Permanent International Ornithological Committee (PIOC) was established with 130 members.

Discussions at the 1st Congress fell under three topics: (a) recommendations for international conservation laws; (b) the history of domestic fowl; and (c) establishment of bird observation stations worldwide, the last being the most important to members of the Congress. Emphasis was placed on the establishment of avian observation stations to record the migration of birds in different parts of Europe, as well as on the publication of the results (see Blasius and Hayek, 1885; Merrian, 1885). It is unclear from the Congress reports whether papers on other subjects of avian biology were presented. A journal, *Ornis* (14 volumes published, 1885–1907) was established for this purpose, with the long-term object of understanding the routes and timing of bird migration in Europe. Unfortunately, no system was established for analyzing the data, and the project eventually collapsed in the early 1890's under the weight of the disordered mass of information (Stresemann, 1975: 334–335). Even so, this initial push by the 1st International Ornithological Congress led to the establishment of a number of bird stations in Europe and to a great interest by European ornithologists in all aspects of avian migration, a preoccupation that has continued to this day (Bock, 2001: 101–103).

## 3 The next step—the 2nd Congress, Budapest, 17–20 May 1891

The decision was reached at the Vienna Congress to hold congresses every four years; and so the next congress was voted for Budapest in 1888 under the presidency of Otto Herman (Hungary). The congress thus remained in the Austro-Hungarian Empire, under the continued patronage of Crown Prince Rudolf, but was postponed to 1889, and was delayed further by the unfortunate death of Crown Prince Rudolf in January 1889. At the urging of Victor Fatio

(Switzerland), the 2nd Congress finally opened on 17 May 1891 at the National Museum of Hungary. Considerable effort went into inviting ornithologists from many countries; hence the Budapest meeting moved quite far toward the format of an international congress as we know it today, with members from more countries, including Louis Bishop and Arthur Chadbourne from New York, United States, and several ornithologists, including R. Bowler Sharpe and Philip Lutley Sclater, from the United Kingdom. A rather full program of contributed papers was offered, as well as a series of major lectures by well-known ornithologists such as R. B. Sharpe, M. Fürbringer, J. A. Palmén and A. Newton. Those by Sharpe (1891) and Fürbringer (1891) were published as separate monographs, the former independent of the congress proceedings while that of Fürbringer (who could not attend at the last minute because of serious illness of his son) was issued as an integral part of the Proceedings.

As usual in early congresses, the election of officers was held at the meeting. Professor Victor Fatio and Dr. Otto Herman were elected as Co-Presidents and Dr. Geza von Horváth (Hungary) as Secretary-General. Somehow in the proceedings of later congresses, the existence of a Secretary-General for the 2nd Congress has been overlooked, and it is time to give Dr. Horváth his proper due. It should be noted that the position of the Secretary-General (sometimes simply listed as Secretary) in the early congresses differed from its role in post-World War II congresses in which the Secretary-General was responsible for all aspects of organizing and running the congress and for publishing the proceedings. In earlier congresses, the duties of the Secretary-General are not very clear, and may not have involved much more than editing congress proceedings. Early congresses were also served by a *Schriftführer*, in the sense of Recording Secretary; this position differs from that of Secretary-General insofar as the *Schriftführer* records the actual proceedings of the meeting, as still done today at the annual meetings of the Deutschen Ornithologen-Gesellschaft. The change from the earlier role of the Secretary-General may have begun at the 6th Congress in Copenhagen, 1926, but it appears to have been completed only from the 9th Congress in Rouen, 1938. Since World War II, the Secretary-General has been responsible for the organization and running of the congress and for the publication of proceedings.

Most interesting at the 2nd Congress was the election of S. de Xántus as Sergeant-at-Arms—an event unique for international ornithological congresses. It is difficult to understand why such an official would be needed at a scientific meeting, although

there have been instances at congresses when a Sergeant-at-Arms would have been useful. I can recall one at the 1978 Congress in Berlin, where a Sergeant-at-Arms might have been needed had not an overly crowded lecture hall kept the two adversaries apart. And possibly with some of the strong differences of opinion at the 2nd Congress on the organization and future of congresses, a Sergeant-at-Arms might definitely have been needed. Thirty Honorary Members of the Congress, headed by Fürsten [Prince] Ferdinand of Bulgaria, were also elected. Prince and later King Ferdinand of Bulgaria (and following his abdication in favor of his son in 1919—he was known as Graf Murany of Sachsen-Coburg-Gotha) attended all international ornithological congresses, often in honorary positions, from the 1st in 1884 until the 9th in 1938.

Aside from its delay, considerable problems surfaced at the 2nd Congress, most arising from a clash in personalities and ideas about congress structure and content (see Stresemann, 1938: 10–13). The discord is reflected in the publication of a separate report on the Congress by Blasius (1891), who was the President of the PIOC but not of the 2nd Congress. Some of it lay in the planning of future congresses which was affected by difficulties in on-going migration studies as a central theme and the lack of finance to continue it. But a large part of the discord came from a push by newer members of the PIOC to introduce a program of papers on a broad spectrum of topics covering all aspects of avian biology, not just migration. As noted by Stresemann (1938: 13), further problems resulted from the lack of a clear, workable set of statutes and of a governing body between congresses. A Permanent International Ornithological Committee existed, but it was too large a body to operate efficiently between congresses.

Furthermore, the President of the PIOC, who at that time was Professor Rudolf Blasius, was not the President of the Congress itself. Clearly this awkward arrangement of officers may have been responsible for some of the problems in the 2nd Congress. A new and more broadly based Permanent International Ornithological Committee was elected. Moreover, the potentially confusing arrangement of officers was resolved when Professor Emile Oustalet was elected President of the 3rd Congress, in advance. Professor A. B. Meyer presented a detailed organizational plan and set of statutes, but these were not acted on, and I am unaware that they were ever published. Yet in spite of these shortcomings, the communal spirit of ornithologists prevailed and the decision was reached to schedule the next congress in 1895, four years in the future under the presidency of Dr. Oustalet. Even then, because of the timing of the world fair in

Paris, the 3rd International Ornithological Congress was delayed until 1900.

Two further consequences of the second Congress were first the establishment of the Hungarian Ornithological Society in 1893 and its journal *Aquila*, and secondly the adoption of new rules of ornithological nomenclature (Blasius, 1891: 300 – 308). This saw the Strickland Code replaced by one drawn from the Code of the American Ornithologists' Union (Stresemann, 1938:12). The new rules were based on an absolute application of priority, and in the opinion of some congress members “no greater blow at the much desired uniformity of nomenclature was ever delivered” (Alfred Newton). Adoption of these rules at the 2nd Ornithological Congress took place just prior to the adoption of the Rules of Zoological Nomenclature at the Fifth International Congress of Zoology in Berlin, 1901, the latter having authority to supersede the rules accepted at the Budapest Congress. Lastly, an excursion was available for congress members for the first time. To my knowledge, all subsequent congresses have included excursions for the members, becoming an important part of the meeting for many members and permitting them to see interesting and often unique environments and birds in the congress region.

#### 4 A new direction—the 3rd Congress, Paris, 26 – 30 June 1900

After a long delay of five further years, the 3rd Congress finally met in Paris under Dr. Emile Oustalet (France) as President, G. Jean de Claybrooke (France) as Secretary-General, and with a larger number of members, most from France, Germany, Belgium and the Netherlands, but also including William Brewster (Boston) and a Miss Juliette A. Owen (St Louis) from the United States. This Congress set new directions and established the basic format for all future congresses. A large number of contributed papers were presented. The Proceedings still contained a long official report (pp. 1 – 140); but the remaining pages (141 – 495) were devoted to papers presented. And the work of the Congress went smoothly, a broader representation of ornithologists attended, and the difficulties experienced by the previous meeting were either solved or caused no problems. The 3rd Congress was also the first one in which “lantern slides” were used.

No question arose about planning for the next congress, the decision being made to hold them every five years. Dr. R. Bowdler Sharpe (United Kingdom) was elected President of the following 4th Congress, to be held in London in 1905; and new members were elected to the Permanent International Ornithological Committee. The necessary organiza-

tion for the 4th Congress was established with cordial relationships maintained between Professor Oustalet, President of the 3rd Congress, and Dr. Sharpe. Because of his ill health, Sharpe persuaded Oustalet to continue as President of the Permanent International Ornithological Committee and as editor of the *Ornis*. Dr. Sharpe was able to assume his duties as president only late in the autumn of 1904, but still in time to be able to organize the 1905 London Congress with his co-workers. The Paris Congress was the first attended by Dr. Ernst Hartert who played a central role in re-establishing the congresses in the aftermath of World War I.

Basic organizational problems were finally solved at the Paris Congress with the adoption of Statutes for the Permanent International Ornithological Committee (Proceedings, pp. 101 – 109). With such a well-defined set of rules, and, more importantly, with the good will of the international community of ornithologists and a strong impetus for ornithological congresses, problems besetting the continuity and growth of congresses fell away\*. The difficulties of the 2nd Congress became a thing of the past and can be attributed to the usual problems faced by the forming of any new scientific organization, especially one that is international. By the end of the 3rd Congress, strong traditions had been established which were sufficient to guarantee continuity for the next century, in spite of the disruptive effect of two world wars.

#### 5 Ongoing development—the 4th Congress, London, 12 – 17 June 1905, and the 5th Congress, Berlin, 30 May – 4 June 1910

The Secretaries-General Dr. Ernst. J. O. Hartert (United Kingdom) and J. Lewis Bonhote (United Kingdom), with the assistance of an efficient local committee, planned the London Congress in a reasonably short time. A detailed summary of all sessions of the Congress is included in the Proceedings, as well as the papers presented. As to be expected, a large number of members came from the United Kingdom, and they were augmented by a good representation from the rest of Europe, five from the United States and 3 – 4 from South America, though none from Canada. Carl Hellmayr was listed from Tring, England. Interesting is that no less than 8 Misses Sharpe

\* But see the comments of Stresemann (Proceedings, 1938: 12 – 13) on the difficulties of adopting and using governing statutes for the PIOC and congresses, and his uncertainty as to whether the statutes employed at one congress, the 8th, would remain in force until the next, the 9th. They did, and remained in effect until new statutes and by-laws were enacted in Berlin in 1978.

were members of the 4th Congress, of which at least five must have been unmarried daughters of R. Bowdler Sharpe as they were entered with the same address.

On the opening day following welcoming formalities and the election of a series of vice-presidents, the Congress was organized into five sections under formal officers (a procedure that lasted until the 9th Congress, 1938). President Sharpe gave the first presidential address for ornithological congresses, a tradition that has continued to the present day (Proceedings, pp. 90–143). He presented a detailed history of the bird collection of the British Museum, to be followed next day by Frank M. Chapman's lecture on the nature of museum collections of birds, based on that of the American Museum of Natural History, New York City. Needless to say, many papers dealt with avian systematics and nomenclature. Professor R. Blasius presented a detailed analysis of nomenclature (pp. 35–37; 275–288) which was discussed fully, though no resolutions were passed in deference to the pending action of the International Zoological Congress (see Bock, 1994: 33–34).

Economic Ornithology and Bird Protection was another major topic raised and involved a general discussion at the General Meeting of 17 June (pp. 31–32). At that meeting, Walter Rothschild called attention to the slaughter of nesting penguins on islands south of Australia and New Zealand; the birds were "boiled down for oil." If continued, the penguin populations of these islands would be doomed to extinction. Rothschild proposed the following strongly-worded resolution, seconded by Sir Walter Buller: "That telegrams be sent in the name of the Fourth International Ornithological Congress to the Commonwealth of Australia and the Governments of Tasmania and New Zealand, appealing to them most strongly to pass legislation to prevent the destruction of Penguins and all other birds which were boiled down for oil on the islands under their rule."

If anything could be said about the 4th Congress, it would be that it was opulent. Members of recent congresses would have scarcely recognized it. I quote from the report of the general meeting (Proceedings, p. 30):

"Thursday, June 15th."

"This day was devoted to an excursion to Tring, the members of the Congress, being the guests of the Hon. Walter Rothschild, M.P."

"A special train left Euston Station at 9 o'clock. The members of the Congress were conveyed from the station to Mr. Rothschild's museum in brakes. An hour was devoted to a walk through the Museum, and then the party proceeded to the Victoria Hall in Tring where Mr. Rothschild delivered his lecture on

'Extinct and Vanishing Birds.' The hall was decorated with flowers and plants, and along the walls was exhibited a large collection of birds either extinct or more or less in danger of extinction, as well as skeletons, bones, and drawings."

"Luncheon followed, after which photographs were taken on the lawn, and the party divided, some to see the birdskins or eggs at the Museum, under the guidance of Dr. Hartert and Mr. Hellmayr. Others, led by Mr. Rothschild, visited the park, to see the Rheas, Emeus and Kangaroos, others again driving to the 'Tring Reservoirs,' where they saw numerous wild Ducks and other Water-fowl. At 5 o'clock tea and light refreshments were served at the Bungalow, and at 7:10 the special train left Tring station again for London."

Not having an OED at hand, I have no idea what type of vehicles "brakes" were, but presumably they are horse-drawn carriages or wagonettes considering the date of the London Congress. The "Bungalow" was most likely a wooden building with a veranda around the front and sides as found in many of the British colonies. Hopefully the day for the excursion to Tring was a sunny one. In the evening of 14 June, "...a conversazione was held at the Natural History Museum"; in the afternoon of 16 June, a reception was given by the Lord Mayor of London at Mansion House; and that evening a dinner for Congress members was hosted by the British Ornithologists' Union at Frascati's Restaurant. Excursions occupied three days at the conclusion of the Congress: on the 19th to Woburn Park in Bedfordshire, the home of the Duke of Bedford, on the 20th to Cambridge and the university where they were hosted by Professor A. Newton, and finally on the 21st to Bampton with its cliffs of nesting birds. Climbers brought up a number of eggs which were purchased by some members of the Congress for their collections, an event that would not only eschewed by future congresses in the later 20th century, but roundly condemned.

At the final General Meeting in London, President Sharpe presented a resolution from the Permanent International Ornithological Committee that the next Congress be held in Berlin in 1910, with Professor Anton Reichenow as President; and if that was not possible, the Congress was to be held in Belgium, with Professor A. Dubois as President. The Proceedings of the 4th Congress constituted the final volume, number 14, of *Ornis*. It should be noted that Dr. G. Radde, President of the 1st Congress, had passed away in 1903, and that Dr. Victor Fatio, Co-President of the 2nd Congress, and Professor E. Oustalet, President of the 3rd Congress, were members of the 4th Congress but died before the Proceedings were published. Dr. Sharpe himself did not live to see the

5th Congress, passing away on 25 December 1909.

The Berlin Congress in 1910 took place as planned and was as successful as the 4th in London. This time most members were from Germany; but though there were still very few, possibly only three, from North America, the first Canadian member, J. H. Fleming, attended. The 5th Congress was the first attended by Erwin Stresemann, a prominent member of all successive congresses until the 15th Congress in The Hague in 1970, perhaps the longest running record for any ornithologist attending successive congresses. King Ferdinand of Bulgaria (after 1919, known as Graf Murany of Sachsen-Coburg-Gotha) attended all congresses from the first to the ninth over a period of 54 years. Again, the official report of the Congress was long, 114 pages; but another 1 000 pages were devoted to papers presented. These included an important presentation by O. Heinroth on the ethology of ducks, and a major paper by Lucanus on avian physiology. Innovations at the 5th Congress were the first movie film on birds and the first sound recording, which was of a nightingale. Films of birds became an important part of later congresses until the 21st Congress in Vienna, 1994 when they were dropped from the program. Hopefully, films will again become a part of future congresses, from the next one in Hamburg, 2006.

The projection of the 6th Congress in 1915 was prophetic in a sad way. Sarajevo, Bosnia, was chosen as the congress site under the Presidency of Dr. Otmar Reiser. But the assassination of Archduke Francis Ferdinand in Sarajevo, 28 June 1914, precipitated World War I—and the end to plans for the Congress. The resulting gap of 16 years until the next congress in 1926 was the longest in the history of international ornithological congresses.

## 6 A new beginning—the 6th Congress, Copenhagen, 24–29 May 1926

After the end of World War I, the major problem facing the revival of international ornithological congresses was that most leading ornithologists in Europe lived in countries on opposite sides of the past conflict; and no ornithologists outside of Europe had been deeply involved in the activities of earlier congresses. The decision reached at the 5th Congress to hold the next one in Sarajevo was no longer viable. The Permanent International Ornithological Committee was in disarray, as were its Executive Committee and the officers elected at the 5th congress in 1910. Nor did the existing Statutes of the PIOC provide any solution to the impasse. A country that was neutral during WW I had to be found; and more importantly a person acceptable to ornithologists generally had to come forward to take charge. The latter was Dr.

Ernst Hartert, originally a German ornithologist but who had worked in Walter Rothschild's museum at Tring, England, since the last years of the 19th century. Hartert was highly respected in ornithology because of his far-sighted systematic work and monumental treatment of the birds of the Palaearctic region (Hartert, 1903–1922). Moreover he had played a major role in both the 4th and 5th Congresses, chairing the meeting of the PIOC at the latter. With the assistance of Danish ornithologists, he now pushed forward to organize the long delayed 6th Congress in Copenhagen. His work, as well as the great efforts of Danish ornithologists, was recognized in glowing tributes in the Congress Proceedings by Schiöler and Lönnberg (pp. 17–19).

The Copenhagen Congress proved a great success and brought together once again ornithologists from many European countries, as well as from North America (Fleming from Canada and 5–6 from the United States, including Carl Hellmayr who was now in Chicago) and a scattering of members from other countries. The presidential address by Hartert, "On the development and progress of ornithology since 1910" (Proceedings, pp. 35–51), stressed systematics and mentioned only briefly the fields of animal behavior, anatomy and breeding biology, with slightly longer statements on avian migration and conservation. He also listed a large number of ornithologists who passed away since the last congress in 1910. No mention was made of the International Council for Bird Protection which was founded in 1922 in London.

The Proceedings of the 6th Congress differed from those preceding it in that much less space (35 out of 641 pages) was devoted to official reports, including summaries of the sections and papers. The decision was reached to hold international ornithological congresses every four years. For the next in 1930, invitations were received from The Netherlands, Finland and Tunis, the vote going to The Netherlands, with Professor E. Lönnberg as President. The 6th Congress had revived the ornithological congresses after the long hiatus of 16 years, a great initiative that, although drawing on the strong international interests of many ornithologists, would not have been possible without the major efforts of Ernst Hartert. The credit for the continuation of the congresses must go, in the final analysis, to him.

## 7 Continuing Progress—the 7th Congress, Amsterdam, 1–7 June 1930, 8th Congress, Oxford, 2–7 July 1934, and 9th Congress, Rouen, 9–13 May 1938

The 7th Congress in Amsterdam with Professor A. J. E. Lönnberg (Sweden) as President and Pro-

fessor L. F. de Beaufort (The Netherlands) as Secretary-General took place without problems and, as far as I can find, without innovations. It was smooth-sailing after the successful 6th Congress. Several major lectures were given, much in the nature of the plenary lectures of later congresses. These included E. Stresemann (pp. 53 – 72) on the “Progress of anatomical and physiological studies of birds,” K. Lambrecht (pp. 73 – 99) on “Progress in paleornithology,” and H. Duncker (pp. 215 – 243) on “Avian genetics,” the last not mentioned by Birkhead (2003) in his history of Duncker’s work. The official report of the Congress was short, covering pages 1 – 50, of which pages 6 – 29 comprised the presidential address. Four resolutions were passed: (1) for removal of bounties on birds of prey, (2) against discharge of oil at sea, leading to the destruction of sea birds, (3) for protection of the quail *Coturnix coturnix*, and (4) for protection of *Egretta alba* in southern Europe.

The 8th Congress was set for England in 1934, thereby fixing a four-year cycle for congresses, with Professor E. Stresemann (Germany) as President and the Reverend Francis C. R. Jourdain (United Kingdom) as Secretary-General. Although it was originally scheduled for London, the Local Committee, under the new Congress Statutes, voted to change the venue to Oxford where the facilities of the University were available. It is most interesting to compare the 4th, the 8th and the 14th congresses, all held in the United Kingdom and all reflecting their times. The 4th was simply lavish compared to the 8th which was austere and much closer to the experiences of present-day ornithologists attending post-WW II congresses, including the 14th Congress at Oxford in 1966.

The first item of importance (Proceedings, p. 1) is that a small committee, consisting of P. R. Lowe, W. L. Sclater and F. C. R. Jourdain, met to draw up “a code of rules for the congress.” It was submitted to the members of the International Ornithological Committee, approved by a large majority, and then printed and circulated prior to 1933. However, to my knowledge, this set of rules was never published at that time which may have contributed to the concern expressed by Stresemann in his presidential address (Proceedings, p. 13). A Permanent Executive (= Permanent Executive Committee [PEC]) was established under the new rules, consisting of the President (Stresemann), and five elected members (Lönnerberg, Sclater, Wetmore, van Oordt and Berlioz); it was increased to six members (de Beaufort) at the Oxford Congress itself. The Secretary-General (Jourdain) was not a member of the Permanent Executive, but served as its secretary, an arrangement that lasted until the 17th Congress in

1978. Graf Murany, Admiral H. Lynes and Professor E. Lönnerberg were elected Vice Presidents.

The red grouse *Lygopus scoticus* was adopted as the emblem for the 8th Congress, the first designation of a congress symbol. The Congress was arranged in four sections (Proceedings, p. 23): (1) systematics, biogeography, paleontology and general biology; (2) anatomy, physiology, embryology and genetics; (3) migration and locomotion; and (4) aviculture, protection and agricultural ornithology. The sections met concurrently on the four congress days. As usual, formal officers for each section were established at the beginning of the Congress. There was a meeting on 5 July of the International Committee (presumably, Council) for Bird protection, but no report appeared in the Congress Proceedings.

The Official Report for the 8th Congress, as for the previous two, was short, of only 48 pages in the Proceedings, of which the Presidential Lecture by E. Stresemann covered pages 6 – 23. His address reviewed the history of the first 50 years of International Ornithological Congresses, and was useful to me in compiling this narrative. Individual papers covered pages 49 to 761, and included several important ones. W. Meise (1938) examined progress in systematic ornithology since 1920 in the longest paper ever published in a congress proceedings (141 pages). In it, he reviewed the status of new species described since that date. Collations of new avian species have been continued since by Mayr and his associates, beginning with Zimmer and Mayr (1943) up to Vuilleumier, LeCroy and Mayr (1992), in six updates. A new up-date is overdue. K. Lorenz presented his first observations on the social behavior of the jackdaw *Corvus monedula*, J. Delacour reviewed the classification of the Anatidae based on courtship behavior, M. M. Nice discussed the life history and population dynamics of the song sparrow *Melospiza melodia*, J. S. Huxley addressed threat and warning coloration in birds, and B. Stegmann gave a thoughtful assessment of possible biogeographical dispersal of tropical avian groups across the present-day Atlantic Ocean.

New members were elected to the International Ornithological Committee, and the “Permanent” was dropped from the title. Membership of the new IOC was set at 100 which is large, given that only 198 members attended the Copenhagen Congress (1926), 291 the Amsterdam Congress (1930) and 311 the Oxford Congress (1934). The size of the International Ornithological Committee (IOC) of post-World War II congresses became significantly smaller in proportion to congress membership as the number of ornithologists attending increased greatly up to the present time; but the IOC retained its traditional size of

100 members until the adoption of the new statutes and By-laws at the 1978 Congress in Berlin. Invitations for the 9th Congress were received from France and Switzerland, and France was accepted, with Professor Alessandro Ghigi as President and Jean Delacour as Secretary-General. The Permanent Executive Committee then consisted of the President, the Secretary-General, and five elected members representing Germany, Great Britain, France, the Scandinavian countries and middle-European countries. Majority representation on the PEC from specific countries in Europe lasted into the 1980s, even after the addition of members to cover North America, South America and Australasia.

At the Oxford Congress, resolutions were passed on the pressing matter of oil pollution at sea, and to urge the study of avian biology “as leading to the development of the sense of observation and in consequence to the development of the spirit of protection of birds.”

A committee was also appointed (Proceedings, pp. 28–29) under the chair of Professor E. Stresemann “to deal with the question of nomenclature and fixation of names where strict adherence to the law of priority would result in greater confusion than uniformity.” This committee was the precursor of the present-day Standing Committee on Ornithological Nomenclature which was reconstructed at the Basal Congress in 1954. It is unclear whether the committee appointed in 1934 ever acted on any questions of ornithological nomenclature; no such actions were published in the Congress Proceedings.

Excursions followed the formal sessions of the Congress with a unique event, namely a long excursion to the islands of Skokholm, Skomer and Grassholm in two Royal Navy destroyers, the *Wolfhound* and the *Windsor* which were made available to Congress members. The weather was good, the seas calm and all comforts were made available for the sea-faring ornithologists, including deck chairs. At one point shortly after leaving Grassholm, the uncharacteristic signal for the British navy was made from the *Windsor* to the *Wolfhound*: “Alter course to line ahead to engage *Puffinus puffinus puffinus*.” (Proceedings, p. 33). Landings were possible on the islands, and the party was able to lunch on Skokholm.

The 9th Congress in Rouen, with Professor Alessandro Ghigi (Italy) as President and Jean Delacour (France) as Secretary-General, met successfully on schedule in 1938, with post-congress tours to Paris and then the Camargue at the delta of the Rhone River in the south of France. Dr. A. Wetmore was added to the Permanent Executive Committee. The organization and running of the Rouen Congress went

very smoothly, as testified by a very brief report in the Proceedings. The Congress itself was again divided into four sections, namely (1) taxonomy and zoogeography, (2) anatomy, physiology and embryology, (3) general biology, and (4) applied ornithology. The International Council for Bird Protection (ICBP) met in Rouen on 6–8 May immediately before the 9th Congress. The Proceedings for the 9th Congress were published very quickly, dated 1 October 1938, in the same year as the publication of the Proceedings of the 8th Congress. It included a very brief official report and the texts or abstracts of papers presented.

The most important achievement of the 9th Congress was the publication of statutes for the IOC and its congresses under the title *Règlement des Congrès Ornithologiques Internationaux* (Proceedings, pp. 535–536). These were the rules approved in 1932–1933 by a majority of the members of the IOC and mentioned in the Proceedings of the 1934 Congress as printed and approved but not published then (Proceedings 1934:1). Although these rules are always cited as the Rouen *Règlement*, they were not adopted at the Rouen Congress as usually stated or implied. The *Règlement* established the size of the IOC at 100 members, hence the traditional name of “the Committee of One Hundred.” The Permanent Executive Committee consisted of the President, and six elected members (but not the Secretary-General who remained as secretary for this committee); it acted for the IOC during the inter-congress periods. Little is said about the duties of the President and the Secretary-General. An assessment (? = subscription) was levied on the members of the IOC, but it is unclear whether it was ever collected, unless “assessment” meant “registration fee”, in which case the amount subsequently rose rapidly above the amount stated.

The 10th Congress was set for the United States in 1942 (although this decision was not stated definitely in the Proceedings of the 9th Congress); Alexander Wetmore (USA) was appointed President and L. Griscom (USA) Secretary-General. But this Congress was not to be; World War II began in Europe in September 1939. Although another interruption to the congresses ensued, it turned out to be nowhere near as long as the lapse after World War I.

## 8 A second ‘new’ beginning—the 10th Congress, Uppsala, 10–17 June 1950

Re-establishing international ornithological congresses after the break caused by World War II was much easier than after World War I because of the existence of a Permanent Executive Committee which



could act for the IOC under the Rouen Règlement. It was clear to everyone that it would not be possible to hold the 10th Congress in the United States as decided at the Rouen Congress because of the economic difficulties faced by European members traveling to North America. In lieu, the Swedish Ornithological Association was asked if they would host the 10th Congress in 1950; and they accepted on 5 March 1949 with the assurance of financial support from the Swedish Government. Sweden was one of the few neutral European countries during World War II and hence a congress there was readily acceptable to all ornithologists. The PEC appointed Professor Sven Hörstadius (Sweden) as the Secretary-General; Dr. Alexander Wetmore (USA) continued as President. An Organizing Committee was established and the decision made to hold the Congress at Uppsala where it would be possible to use the facilities of the university. About 6 500 invitations were sent out between July and September 1949 to individual ornithologists, museums of natural history and ornithological societies, announcing the Congress in June, 1950, providing information about the program, information about Congress costs and information on registration for the Congress and the various tours. Response was good, with 377 ornithologists fully registered and 337 attending.

And although no mention was made in the Proceedings, the raven *Corvus corax* was evidently chosen as the symbol of the Congress, as indicated by the pair shown on the title page of the Proceedings. The ICBP also held its first meeting since World War II at Uppsala in the days just preceding the Uppsala Congress on 8–9 June.

In addition to the Presidential Address and a special lecture on “Introduction to Swedish ornithology” by Secretary-General Hörstadius, four special lectures were presented by Dr. Ernst Mayr (avian speciation), Professor Jean Dorst (migration), Dr. Niko Tinbergen (behavior) and Dr. David Lack (ecology). These were in the form of plenary lectures that became established at later congresses. Ernst Mayr’s lecture was read by Dr. R. C. Murphy as Mayr was unable to attend because he could not to obtain his new US passport in time and he would not travel on his old German passport. Following each of these special lectures were series of papers in the form of a symposium on the general topic of the major lecture; but no mention was made in the proceedings on the exact nature of these supplementary lectures and the lectures were not published together as symposia. Three full evening film programs were presented, as well as a full-day Round Table Conference (= the Round Table Discussion of modern congresses) on Friday, 16 June.

Following a paper on the nomenclatural controversy over the generic name *Colymbus* Linnaeus 1758 by Finn Salomonsen (pp. 148–134), a special session of the Congress was arranged at which a committee (= the future Standing Committee on Ornithological Nomenclature) was established to inquire into such intricate cases, and to propose ways of stabilizing avian nomenclature by establishing *nomina conservanda*. Apparently the decision to establish such a committee at the 1934 Oxford Congress had been forgotten.

Wednesday, 14 June was a free day, celebrated by a bus excursion to a coniferous forest and fen region north of Uppsala, from which the first group of buses left at 12:00 midnight on Tuesday evening and the second at 2:00 pm on Wednesday afternoon so that congress members could experience the long twilight in northern Europe close to Midsummer’s Day. A series of pre- and post-congress tours had also been organized, from the southern tip of Sweden to northern Swedish Lappland.

Invitations for the 11th Congress in 1954 were received from India, Italy and Switzerland, of which that from Switzerland was accepted. Dr. A. Landsborough Thompson (United Kingdom) was elected President. In addition to the president, seven members were elected to the Permanent Executive Committee; the Secretary-General elect, Professor A. Portmann (Switzerland), was its secretary, but not a member of the committee. The Uppsala Congress proved a great success, organized at short notice and run without any signs that 12 years had elapsed since the 10th Congress in Rouen. The greatest change was language; a majority of papers in the Proceedings were in English which had become the international language in science after 1945. It was a trend that was to continue ever more strongly in ensuing congresses.

## 9 Continuing in Europe—the 11th Congress, Basel, 29 May–5 June 1954 and the 12th Congress, Helsinki, 5–12 June 1958

Drawing on experience from the successful 10th Congress, the organization and running of the next two congresses went very smoothly. A decision was reached to hold the 11th Congress in Basel, with Professor Adolf Portmann appointed as the Secretary-General under whom efficient National and Local Committees were established. In 1953 some 6 000 invitations were sent out around the world, with the result that 616 ornithologists registered for the Congress from 40 countries. The seriously endangered northern bald ibis or waldraap *Geronticus*

*eremita* was chosen as the emblem for the Congress. In addition to the Presidential address by Dr. Lansborough Thompson, special lectures on “The World of Birds in the Alps” (Dr. U. Corti) and “The evolution of the avifauna of Switzerland” (Dr. P. G  roudet) were presented, together with a series of five plenary lectures and three symposia in addition to a large number of contributed papers in 6 sections and a number of films. Clearly a pattern of plenary lectures and symposia was emerging for the scientific program of ornithological congresses.

As in previous congresses, the ICBP met just before the Basel congress in 23 – 28 May 1954. A meeting of the International Committee for Bird Ringing took place during the Congress, as did a Conference on Classification and Nomenclature of European Birds (p. 45). The latter generated considerable controversy because the charge to this committee was to consider the classification of birds to be followed in European publications. One outcome was the forming of a subcommittee to decide on the sequence of families within the Passeriformes; this subcommittee included only European-trained ornithologists. Even so, the editors (see Mayr and Greenway, 1956) of Peters’ *Check-list of Birds of the World* (see vol. IX: vii, 1960) pledged to follow its recommendations for the Oscines. The resulting sequence differed considerably from the “American system” advocated by Wetmore and followed by most New World ornithologists, and aroused considerable argument and opposition (Bock, 1990). Such actions, together with the resulting controversy, show that care must be taken in reaching and advocating decisions at international ornithological congresses; decisions will not necessarily be accepted by all ornithologists, no matter how carefully the committee is appointed and does its work. A second subcommittee was also established at the conference to decide on genera, species and subspecies of European birds, but it is not certain whether this group ever took action.

The standing Committee on Ornithological Nomenclature was reappointed, although without a report of their activities in the Congress Proceedings. Their decisions were published instead in the *Bulletin of Zoological Nomenclature* 9 (1952): 1 – 106 (Salmons  n, 1960: 30).

Changes were made in the composition of the PEC, expanding it to eight members in addition to the President. It was determined that no more than two members could be elected from any one country, and that no elected member could serve for more than two successive terms. The Secretary-General was to be appointed by the country hosting the congress and to serve as the secretary of the PEC, but without being a member. A proposal was also put forward for

the IOC to become a *Sub-Section of the Section of Zoology of the International Union of Biological Sciences* jointly with the International Council for Bird Protection. The IOC became a subsection of the Section of Zoology, but it is not clear whether the ICBP has participated as well.

Two all day excursions were held on mid-congress free days, as well as a series of 11 pre- and post-congress tours to all parts of Switzerland.

Invitations for the 12th Congress in 1958 were received from South Africa and Finland, with the IOC voting to accept that from Finland because of continuing problems of travel costs for most European ornithologists. Professor Jacques Berlioz (France) was elected President. Work started quickly on the 12th Congress, the Finnish Ornithologists’ Union deciding that the congress was to be held in Helsinki, appointing a Finnish Executive Committee and nominating Professor Lars von Haartman (Finland) as Secretary-General. His wonderful dry sense of humor can be found throughout the official Report of the congress.

The Helsinki Congress opened with the Presidential Address by Professor Jacques Berlioz—the fourth emphasizing the role of museum collections in the study of ornithology—followed by a lecture on the distribution of Finnish birds by Professor P. Palmgren and another by Professor C. A. Willemssen on the falcon book (actually an early treatise on avian biology) written by the Emperor of the Holy Roman Empire, Kaiser Friedrich II); unfortunately the last paper was not published in the Proceedings. No additional plenary lectures were given, but three symposia were organized, the first by E. Mayr on “Adaptive evolution of birds” (Proceedings, pp. 10 – 11, 495 – 498), the second on “Avian classification” (Proceedings, p. 11), and the third on “Nocturnal migration” (Proceedings, p. 11 – 12). A series of papers on the physiology of migratory birds by Schildmacher, Merkel, Odum and Wolfson (Proceedings, p. 12) could be considered a fourth symposium. Because the papers in the Proceedings were arranged alphabetically by author, it is not easy to determine the contributions to each symposium. The heading on left hand pages does give the subject of each paper, but these are not always accurate, e. g. J. M. Cullen’s paper on adaptive evolution is listed under behavior and life history. I could not find any papers from the symposium on avian classification. The paper by Ernst S  tter was not published, but it must have been similar to the one he presented the following fall at the 75th anniversary of the American Ornithologists’ Union in New York City on the use of radar to observe avian migration—a technique which radically changed the study of nocturnal avian movement.

A long meeting of the Standing Committee on Ornithological Nomenclature was held and fully reported (Salomonsen, 1960). Professor Salomonsen had taken over as chair of this committee from Professor Stresemann in 1955 when the latter was overly occupied with other work. In anticipation of changes to appear in the imminent second edition of the Code of Zoological Nomenclature, in which family-group names were to be covered by rules of nomenclature, the SCON proposed that a large number of avian family-group names affected be placed on the Official List of Names in Zoology (Proceedings, p. 38–39). Unfortunately, this proposal was not acted on by the International Commission on Zoological Nomenclature, leading to many years of hand-wringing by the SCON (Bock, 1994).

As mentioned by Professor von Haartman (Proceedings, p. 11): “the crowded programme of the congress did not allow of any rest in the evening, films being shown as usual.” Three evenings of films formed an interesting part of the program. Two full day excursions, on Sunday, 8 June, and on Tuesday, 10 June, were scheduled, one by bus to Porvoo and the other by boat to the archipelago of Kyrslätt; congress members were divided into two groups so that everyone could experience both. In addition, a series of 9 pre- and post-congress tours were available to all parts of Finland. As usual, the ICBP met on 1–5 June immediately before the Helsinki Congress. A meeting of the Bird Ringing Committee (Proceedings, p. 11) took place in the evening of 10 June, but no report was published. Likewise, a meeting of the International Union for Applied Ornithology (IUAO) (Proceedings, p. 12) took place in the afternoon of 12 June, and again no report appeared. It is not clear from any of the congress proceedings who the IUAO, and their goals, were.

Only a few copies of the two-volume Congress Proceedings were distributed before a major fire at the printers destroyed the remainder. A second printing started at once, in which a few misprints in the first printing were corrected.

After these three most successful congresses, the IOC felt that the general European economy had recovered sufficiently to permit a meeting outside of Europe, and voted to hold the 13th Congress in 1962 in the United States under the presidency of Professor E. Mayr. This decision reaffirmed the earlier decision at the 9th Congress in 1938 to hold the 10th in the United States in 1942. The IOC also maintained the PEC at 8 elected members, without change in the status of the Secretary-General. further it elected new members to bring its strength back to 100 members. It also voted to encourage “... more restrictive international ornithological meetings in the years between

the main international congresses...” These would take the form of continent-wide congresses, of which the first and most successful has been the Pan-African Ornithological Congress. Later the Neotropical Ornithological Congress came into being and has been very successful for all Neotropical countries.

A further comment is needed concerning the decision to accept the invitation of North American ornithologists to hold the 13th Congress in the United States. . The invitation offered at the 11th Congress for South Africa to host the 12th Congress was possibly repeated at the 12th for the 13th Congress in 1962, although there is no mention of it in the Proceedings of the 12th Congress. The decision to hold the 13th Congress in the USA instead was very likely a major factor in promoting Pan-African Ornithological Congresses (Crowe, 1998, 1991). It must be said, however, that, contrary to claims by some South Africans, that the decision to accept the invitation from the United States and not South Africa was taken completely independently of the then recently adopted policy of Apartheid by the government of South Africa. Rather, the IOC felt that it was necessary to honor first its earlier decision to hold a congress in the United States before considering any other invitations. Moreover there was a general feeling that interaction with the large and diverse group of American and Canadian workers was important at this time for the development of international ornithology at the beginning of the 1960's.

By the close of the first 75 years of their history, the international ornithological congresses had gained such strength and importance to students of avian biology that the disruption of World War II caused scarcely a ripple in their continuity. The three post-war congresses were well organized and run without any problems, with progressively increasing attendances. Moreover, an increasing diversity of interesting papers was being presented, with an ever growing coverage of all aspects of avian biology.

## 10 Out of Europe—the 13th Congress, Ithaca, 17–24 June 1962

The three major ornithological societies in North America, the American Ornithologists' Union, Cooper Ornithological Society and Wilson Ornithological Society, joined in inviting the 13th Congress to the United States, with Professor Ernst Mayr (USA) as President and the US and Canadian members of the IOC forming a General Committee for its organization. The first decision was to set the site of the 13th Congress at Ithaca, New York and appoint Professor Charles Sibley (USA) as Secretary-General. A Scientific Program Committee and other committees were quickly established and set to work. As

to be expected, the great auk *Pinguinus impennis*, the symbol of the AOU, was chosen as the symbol for the 13th Congress as well.

Aside from the Presidential address by Professor Mayr, there were no plenary lectures or symposia; all papers were contributed. A special symposium on Birds and Arthropod-borne Viruses was organized by T. S. Work, with a series of contributed papers. Three concurrent sessions were needed to accommodate the papers. The papers presented were grouped under related subjects (Proceedings, p. 4), but the groupings did not correspond exactly with the headings used in the Proceedings. Nor were all papers published. Evenings were devoted to the film program and special discussions (= Round Table Discussions of later congresses). The members of the PEC were elected, as well as new members of the IOC; and the SCON was reappointed for the period of 1962–1966 with Dr. C. Vaurie as the chair. No report was published of their activities for the preceding four years.

Two long excursions were planned, one before and one following the Congress, plus several short ones in the northeastern part of the United States. The short excursions were poorly attended, and two had to be cancelled. An all-day tour was held on Wednesday, 20 June, the free-day, which was followed by a barbecue supper at Taughannock State Park; the weather that day was excellent.

Unfortunately, the Congress report in the Proceedings is so brief that it is particularly difficult to ascertain important actions taken. Of the 1 246 pages in the two volumes of the Proceedings, only 26 pages were devoted to the Official Report of the 13th Congress; and 18 of these pages list committee members, Congress members and delegates. Mention is made that both the IOC and the PEC met twice, but it is not possible to determine which of these bodies reached decisions, such as the vote on the next Congress and its president; clearly they had to have done so. One notable addition to the Report is an account of the finances of the Congress (Proceedings, pp. 5–6), with a reference to more details in the AOU Treasurer's Report for 1961–1962. Financial accounts of congresses are most useful, but such information is commonly lacking in reports of the congresses. As a result there is no way, at present, to compare the costs of the congresses, either as total costs or the cost per member, or to estimate the finances needed for future congresses.

Despite the dearth of official documentation, this first non-European Congress was a great success, attended by 614 regular members out of a total of 879 (Proceedings, p. 6). Probably a majority of the regular members were from the United States and Cana-

da, but a total of 37 countries were represented. At its end, the decision was reached to accept the invitation from the United Kingdom to hold the 14th Congress there in 1966 under the presidency of Dr. David Lack (United Kingdom).

## 11 Back to Europe—the 14th Congress, Oxford, 24–30 July 1966 and the 15th Congress, The Hague, 30 August–5 September 1970

As was the case for the 13th Congress, Official Reports for the 14th and 15th Congresses are very brief, making an analysis of their happenings difficult. A British Executive Committee, its core formed by the British members of the IOC, was convened immediately after the 13th Congress and appointed Dr. Niko Tinbergen (United Kingdom) as Secretary-General. Oxford University was again chosen as the venue for a congress in Britain because of the considerable ornithological research being done there, the numerous smaller rooms for sessions, and the facilities for housing at the various colleges. The robin *Erithacus rubecula*, a bird studied intensively by President David Lack, was chosen as the Congress symbol. The tradition of a mid-congress free day, with several planned excursions, was maintained. A problem of timing, however, existed because of a decision reached at the 13th Congress that congresses in future need “not be held in the breeding season”—though this decision was never mentioned in the Proceedings of the 13th Congress. An offer from the Scottish Ornithologists' Club to host a week-long cruise circumnavigating Scotland from Greenock on the west coast to Leith on the east to observe the seabird colonies finally settled the date of the Congress. The cruise on the *Devonia* took place from 16 to 23 July, with participants traveling by train on the night of 23 July to Oxford in time to register on the first day (Proceedings, pp. xix–xxiii).

Following the Presidential Address “Interrelationships in breeding adaptations as shown by marine birds” by Dr. David Lack, and an equally interesting lecture on the “Adaptive features of the black-headed gull *Larus ridibundus* L.” by Secretary-General Tinbergen, five plenary symposia were held in the mornings and contributed papers given in the afternoons. Only the papers of the plenary symposia were published in the Proceedings. Of contributed papers, not even an indication of the titles and authors is given; these are available only in the abstract volume for the Congress. The congress free-day, Wednesday, 27 July, was devoted to excursions; good weather made these tours pleasant. A film program of two concurrent sessions was held every evening. Meetings of the

following specialist groups were also held: European Ringing Committee, Sea-bird Research, Ornithology of the Western Palearctic, Standing Committee on Ornithological Nomenclature, International Bird Ringing Committee, International Union of Applied Ornithology (IUAO) and a proposal by the President, Dr. Lack, for an internationally agreed world list of birds.

The last meeting was well attended and generated considerable “fireworks”: there was considerable disagreement about the purpose of such a list, how it should be established, whether it should be authorized, and if so, by whom. The meeting was reported anonymously (Proceedings, pp. 365 – 367), concluding that insufficient agreement prevented a resolution to the Congress. It was mentioned that “various leading European ornithologists were making a proposal for an agreed European list, and that in this connection they were entering into correspondence with the editors of the North American checklist.” To my knowledge, nothing further came from this proposal, with the result that today there are diverse world lists of birds, most of them generated for the use of bird watchers.

A report of the SCON is also presented (Proceedings, pp. 369 – 374), summarizing their work over the preceding four years. One major unresolved problem involved avian family-group names affected by the rules in the second edition of the International Code for Zoological Nomenclature (ICZN). The ICZN required a full bibliographic search to ensure correct authorship for each name. Such information on avian family group names and of their priority did not exist in 1966; and none of the members of the SCON felt that they were in the position to undertake such a project. Hence the SCON recommended that ornithologists continue to use all well-established family-group names until such an analysis could be done and well-supported decisions reached. No reports were issued for the other meetings. Nor was any mention made of a meeting of the ICBP in connection with the 14th Congress. One outcome, however, was that the meeting on sea-bird research led to the establishment by the IOC of a Standing Committee on Sea-bird Research (Proceedings, p. xiv, with its initial membership given on page xviii).

Another noteworthy event was the presentation of an Honorary Degree of D. Sc. to Professor Ernst Mayr by Oxford University. Professor Mayr was also honored with an honorary degree by the University of Vienna at the 21st Congress in Vienna, 1994. To my knowledge, he is the only ornithologist to receive such academic honors during an ornithological congress.

In a final paragraph of the Proceedings, we are

told that “As usual, the Permanent Executive Committee met twice, as did the International Ornithological Committee. It was decided that the XV International Congress should be held in The Netherlands in 1970 and Dr. Niko Tinbergen (United Kingdom) was elected as its President.” A listing of the members of the committees of the IOC, and of the IOC itself followed. A brief mention is also made at the beginning of the list of members that those who had not attended the past two congresses, except when prevented by illness, were dropped from membership. The Official Report of 15 pages (over half did not pertain to the work of the IOC or of the Congress), followed by 47 pages of reports from the SCON, the meeting on a world list of birds and lists of delegates and members, is even much too brief to allow any reading between the lines; the lines are simply not there.

Preparations for the 15th Congress started rapidly with a Netherlands Executive Committee selected early; this committee included Professor L. de Beaufort who was the Secretary-General for the 7th Congress in Amsterdam in 1930. The Hague was chosen as the Congress site, and Professor Karel Voous (The Netherlands) appointed as Secretary-General. Other committees, including the Scientific Program Committee, were established. A rapidly expanding membership at the 1962 and 1966 Congresses provided increasing work loads for the Secretary-General and local organizing committees. Even with a large and energetic staff assisting him for the Oxford Congress in 1966, his overall duties, as well as attending to the needs of the International Ornithological Committee and his other work, simply exhausted Secretary-General Niko Tinbergen (Kruuk, 2002: 251 – 252), and led to increased bouts of depression. In spite of his success at the Oxford Congress, Tinbergen was never again a full congress attendee and had to resign his presidency of the 1970 Congress in the autumn of 1969. Professor Finn Salomonsen (Denmark) was elected in his place by the PEC. The change of presidents created no problems for the planning of the Congress and indeed, in 1970, when the 15th Congress was held, it had “two” presidents even though Dr. Tinbergen could not attend. The Eurasian spoonbill *Platalea leucordia* was chosen as the Congress emblem; two birds are depicted in the Congress Proceedings, in a design used for an enamel brooch given to all Congress members.

The Congress program was a very full one, comprising the Presidential Address, six symposia, 33 sectional sessions, 8 special meetings (= Round Table Discussions), 9 committee meetings, and 11 film sessions. The mornings were devoted to plenary sessions — the Presidential address and five of the

symposia. One symposium was held concurrently with the contributed papers in the afternoon; all sessions were held concurrently in the afternoons (Proceedings, pp. 6–10), and 34 films were shown in the evenings. Four satellite meetings, including that of the ICBP, were also held. The mid-week day of Wednesday, 2 September, was a free day, spent on a series of 8 different excursions mostly to view the diverse water-, marsh- and shore- bird fauna of The Netherlands.

Both the PEC and the IOC held two meetings during the Congress. A new By-law was adopted that: “Past-Presidents shall be lifetime members of the IOC, shall be entitled to all rights and privileges of such membership, but shall not be counted when enumerating the 100 members of the IOC.” Two resolutions to the International Commission on Zoological Nomenclature (ICZN) were proposed by the SCON and adopted by the IOC to speed the decision on proposals dealing only with names for birds, namely support for the fifty year statute of limitations and to create the SCON as a formal subcommittee of the ICZN, thereby ratifying the decisions of the SCON. To my knowledge, neither recommendation was accepted by the ICZN. A further proposal was adopted to develop a formal relationship with the International Union of Biological Sciences in which the IOC would become a Section within the Zoological Division. Apparently the proposal made during the 11th Congress in Basel, 1954 was not successful. A committee consisting of J. Dorst, C. S. Sibley and K. H. Voous was appointed to formulate better relationships with the IUBS, as well as bringing the Rules of the IOC up to date; but to my knowledge this committee did not act. The Rules governing the IOC and its congresses, passed by mail vote prior to the 8th Congress in 1934 and first published in the Proceedings of the 9th Congress, Rouen, 1938, remained in effect.

The IOC also voted to accept an invitation from the Royal Australasian Ornithologists' Union to hold the 16th Congress in Canberra, Australia, with Dr. Harry J. Frith (Australia) as the Secretary-General and Professor Jean Dorst (France) as the President. Following tradition, the Secretary-General was not a member of the PEC for the congress in which he served, but was elected to this committee for the ensuing period. This system began at the 8th Congress, Oxford, with the election of Rev. F. C. R. Jourdain to the PEC and continued until the 17th Congress when new Statutes were adopted. The Proceedings for the 15th Congress included the papers of the six symposia and the abstracts of the contributed papers, plus the Official Report for the Congress. All papers in the Proceedings volume, except for the very last abstract by J. Zettel (Switzerland), were published

in English, setting the standard for the future. The antiquated policy of having “Official Delegates” appointed to congresses and listed in proceedings, a practice continued to the 14th Congress, 1966 and which no longer served any purpose, was abandoned permanently at the 15th Congress.

With almost 700 members at the 14th Congress and over 800 at the 15th, and a very full program of morning plenary sessions and a number of concurrent sessions in the afternoons, these two Congresses set the stage for “modern” ornithological congress. Moreover, the 15th Congress set the pattern for holding future congresses outside of the Northern Hemisphere avian breeding season. To this there have been only two exceptions: the 17th Congress in Berlin, 1978 and the 19th in Ottawa, 1986, though the latter was held at the very end of the season.

## 12 To the antipodes—the 16th Congress, Canberra, 12–17 August 1974

The first 15 congresses having been held in the Northern Hemisphere, it was now time to move to the Southern; and so the invitation to hold the 16th Congress in Australia was accepted at The Hague in 1970. President Jean Dorst (France) appointed Dr. Harry Frith (Australia) as the Secretary-General who established the necessary committees for organizing and running the Congress, using many members of the staff of Frith's CSIRO Division of Wildlife Research. The Congress symbol was the magpie goose *Anseranas semipalmata* in a vignette showing three birds to indicate that many males have two females which lay their eggs in the same nest. The Congress was held at the Australian National University in Canberra, ACT. Strikes in the fuel and transport industries caused critical problems for the start of the Congress, leaving many members, including President Dorst, temporarily stranded in various locations around Australia. These problems were dealt with by Secretary-General Frith and his staff in a most expedient way which included a rearrangement of the Congress schedule. The free day was shifted to the first day of the meeting and the opening of the Congress to the second day, by which time the President had reached Canberra from Alice Springs in central Australia.

Despite the distant location of the venue, just over 800 persons attended, including over 500 full members. Complaints were raised by a few European members of the IOC claiming that because of the “remoteness of the Northern Hemisphere countries from Australia many members have been unable to attend the meeting in Canberra”. Accordingly, they felt, absence of northern hemisphere members from the 16th Congress should not count toward the rule that

membership of the IOC lapses after two successive congresses are missed (Proceedings, p. 5). Australian members pointed out, quite correctly, that the distance from Northern Hemisphere countries to Australia was just the same as that from Australia and New Zealand to the Northern Hemisphere, and thus such a modification of the rule should apply equally in reverse. Fortunately these petty proposals were never enacted.

The Proceedings of the 16th Congress are entirely in English, following the trend in international scientific meetings since World War II. In addition to the plenary Presidential Address, the Congress presented 11 symposia containing 61 papers and 130 papers in 9 general sessions. The symposium papers were published in the Congress Proceedings and the abstracts for the contributed papers in *The Emu*, volume 74, supplementary issue. The symposia placed emphasis on aspects of Australian and Southern Hemisphere ornithology, with special stress on the differences in avian biology in the northern and southern continents under the general theme of "The Two Hemispheres." No film program was advertised, but several round table discussions, as well as the meetings of the SCON and the Standing Committee for Seabird Research (SCSR) took place; both committees submitted their reports which were included in the Proceedings. The ICBP also met in Canberra in connection with the Congress.

An important resolution on the scientific collecting of birds for research was passed by the IOC (Proceedings, p. 6), which concluded that the IOC: "*recommends* that Governments allow scientific institutions to collect material they need for research with the requirement that applying institutions, in need of material of endangered species, must ensure that such material is necessary for this research and will not threaten the existence of that population; *invites* the ICBP to endorse this recommendation through its XVI World Conference and also invites the IUBS to consider this recommendation." The Section of Ornithology in the Division of Zoology of the IUBS was established, based on the IOC. The Chair of this Section is the President of the IOC and its secretary is its Secretary-General, the first being Professor J. Dorst and Dr. H.J. Frith. No mention was made in the Official Report of the IOC and its PEC of further work on the Statutes of the IOC as foreshadowed in the report of the 15th Congress.

The IOC also accepted the invitation of the Deutsche Ornithologen-Gesellschaft to hold the 17th Congress in the Federal Republic of Germany, with Professor Donald Farner (USA) as its President. The great success of the 16th Congress demonstrated that ornithological congresses could be held in any part of

the world with a large number of members attending and with a full and diverse program, an essential requirement if congresses are to be truly international.

### 13 Back to Europe—the 17th Congress, Berlin, 4–11 June 1978

Soon after the close of the 16th Congress, the German National Committee voted to hold the 17th Congress in Berlin, the site of the 5th Congress in 1910, and to appoint Dr. Rolf Nöhring (Germany) as Secretary-General. Dr. Nöhring started work on the Congress immediately with Frau Regine Damm as his main assistance and Frau Ingeborg as assistant treasurer. Due to the activity and insight of President Donald S. Farner (USA), the structure of the IOC and the nature of the International Ornithological Congresses changed significantly into the organization that we know today. Significant modifications were the development of a new set of Statutes and By-laws, and the institution of an International Scientific Program Committee (SPC) responsible for the organization of the entire scientific program of the congress.

President Farner, who also held several key positions in the IUBS, had a broad understanding about how international scientific groups should be organized and run. It was clear to him that the existing Rules for the IOC, those adopted in the early 1930s and first published in the Proceedings of the 9th Congress in Rouen, 1938, had become altogether inadequate for specifying the structure of organization and duties of officers and committees of the IOC and its congresses. He formulated a new set of Statutes and By-laws for the International Ornithological Committee, assisted mainly by Walter Bock. These new regulations were the major topic of discussion at a special meeting of the PEC, 11–12 March 1978, at the Airport Hotel, Frankfurt a. M., Germany, and were subsequently adopted by the IOC at its first meeting at the Berlin Congress on 6 June 1978; they became effective immediately. The new Statutes and By-laws (Proceedings, pp. 55–60) then governed the actions taken at the second meeting of the IOC.

At some point, either at the 15th or probably the 16th Congresses, a decision was reached to assign the responsibility for the scientific program for congresses to an international Scientific Program Committee, independent of the Secretary-General and Local Committee. The first such SPC was appointed by President Farner for the Berlin Congress, with Professor K. Immelmann (Germany) as Chair. This committee met for two days in Berlin in October 1975 to formulate the program. Because the Congress was to meet in Berlin, the city where Erwin Stresemann and Oskar Heinroth had worked, and because their lead-

ing students, E. Mayr and K. Lorenz, were still active, the German members of the SPC requested that the Congress include a Stresemann Memorial Lecture and a Heinroth Memorial Lecture to be presented by Mayr and Lorenz respectively. This proposal was agreed to immediately; and in addition to the two Memorial Lectures and Presidential Address, three further plenary lectures were scheduled. Other oral presentations were restricted to symposia, of which 36 were scheduled.

The SPC decided on the subject and the conveners of the symposia, and then turned the work of organization and running of the symposia over to the conveners. The only stricture imposed on conveners was that they were to make every effort to get speakers from different countries, and that no speaker should present a paper in more than one symposium. All contributed papers were restricted to Poster Papers, a decision that caused some controversy, and although all future congresses included poster papers, only the 18th and 21st Congresses restricted contributed papers to this category. A small number of Special Interest Discussions (= RTDs) were held. And there was an excellent and full film program, with many films shown from morning to evening in a designated room.

The Congress was held in the Berlin Kongresshalle, which was located in a large park that permitted quiet walks for congress members during the daily sessions. The building had many rooms suitable for all of the needs of the Congress but lacked sufficient access to restaurants for midday and evening meals. A series of pre- and post-congress excursions were arranged through Europe, extending from southern Spain to Lappland and east to the Danube delta; mid-congress excursions on Thursday, 8 June were restricted to around Berlin. A number of congress members took the opportunity to visit East Berlin.

The IOC adopted the new Statutes and By-laws at its first meeting at the Berlin Congress, as mentioned above. Further, it decided that a member of the PEC should be designated to act as President should the elected President be unable to carry out his duties. In these circumstances, Professor L. von Haartman (Finland) was elected as President and Professor J. Ashoff (Germany) as the designated President for the 18th Congress. An invitation to hold that Congress in Moscow in 1982 had been presented to the IOC at some time prior to the 17th Congress. In their discussion of this invitation in March 1978, the PEC decided that an "emergency" invitation be sought in case the Soviet ornithologists could not present their invitation formally in June at the Berlin Congress. Such a request was made to the

Belgian ornithological community. Both Russians and Belgians presented competing invitations to the IOC at the 17th Congress; the Russians gave strong assurances from the Soviet Government that all foreign ornithologists would be allowed to attend the Congress and its excursions. A spirited discussion followed with a very close vote of 19 for Moscow, 17 for Brussels and 10 abstentions. Immediately following this vote, Secretary-General Nöhring resigned in protest from the IOC, creating history as the shortest tenured Secretary-General in the PEC. New members of the IOC and of the PEC were elected for the term 1978–1982. The Standing Committees for Cooperation of Seabird Research and International Committee for Bird Ringing were voted as official committees of the IOC (pp. 48–49), but to my knowledge the latter did not convene and had to be re-established at the 21st Congress in Vienna in 1994.

There was no formal closing to the Berlin Congress, President Farner saying flippantly at the start of the last day that the last person to leave the congress hall should make certain that the door was closed and locked. The two volume Proceedings of the 17th Congress contained the Official Reports, the papers of the 36 symposia (not all were submitted), the abstracts of the special interest groups, poster papers and films, and the reports of the Standing Committees. It also included an overview of the program, an innovation recommended for all future congress proceedings. With the successful 1978 Berlin Congress, the nature of international ornithological congresses changed markedly to meet the demands of an increasing number of avian biologists attending and the ever broadening areas of research in ornithology. Credit for these progressive changes must go to Donald Farner who worked hard and productively on modifying ornithological congresses and the organization of the IOC into a more modern and efficient format.

And now, I would like to add a final message for the members of the 17th Congress who stood or walked everyday without fear or concern under the large concrete canopy hanging over the main entrance of the Berlin Congress Center Building. Sometime in the autumn of 1978, I saw a photograph of the Congress Center in the New York Times, after its canopy had collapsed but fortunately at a time when the area beneath was empty of people. My immediate reaction was that the collapse had been induced by the meeting of ornithologists during the previous summer; perhaps the structure had been weakened by some of the heated disagreements at meetings of the IOC or at the symposium on "Recent trends in biogeographic analysis" where only the packed lecture room kept feuding speaker and a listener from physi-



cally attacking one another. Or was it the talk on "Reconstructing the curse of speciation" (Proceedings, p. 16) that had the effect. Unfortunately Herr Nöhring missed his chance to include a picture of the collapsed marquee as the frontispiece in the Congress Proceedings, as a memento of such a volatile Congress.

## 14 Behind the 'Iron Curtain'—the 18th Congress, Moscow, 16 – 24 August 1982

The 18th Congress was particularly important as an international event because there had been little communication between the ornithologists of the Soviet Union and most of the rest of the world for many decades, especially since the end of World War II. A congress in the Soviet Union would facilitate direct contact between of these two estranged groups of scientists. But the Congress was equally controversial, as shown by the very close vote at the 17th Congress and immediate resignation of its Secretary-General, Dr. R. Nöhring. Moreover, a letter protesting the Moscow Congress by H. Mueller (1981) was published in *The Auk* with an outstandingly positive answer by D. Farner (1981) who pointed out the immense value of this Congress for building bridges and mutual stimulation of ideas between two such large groups of ornithologists. One convener, S. T. Emlen cancelled his symposium in response to Mueller's letter, but this symposium, on "The origin and evolution of cooperative breeding in birds", was rescued by Professor Russell P. Balda (USA). Professor Lars von Haartman (Finland) proved to be an excellent choice as President, being from a country that was obliged to interact both with the Soviet Union and the West since the end of World War II. The importance of international cooperation in ornithological research was emphasized in the opening statement of the Secretary-General Valery D. Ilyichev (Proceedings, pp. 8 – 14). Accordingly, the symbol for the 18th Congress was the red-breasted goose *Branta ruficollis*, shown in flight against a globe; it is a threatened species migrating from the Soviet Union to winter in Eastern Europe and sometimes northeastern Africa.

Following the 17th Congress, President von Haartman immediately appointed Professor Valery Ilyichev as Secretary-General and the Soviet Organizing Committee with its appropriate subcommittees. He then appointed the Scientific Program Committee under the chair of Professor J. Aschoff (Germany). Some of the non-Soviet members of this committee were able to meet in Frankfurt a. M. in September, 1979, at the annual meeting of the Deutsche Ornithologen-Gesellschaft; Dr. C. Perrins arrived late,

delayed because of the frequent autumn fog in Western Europe. A second, week-long meeting of the SPC was held in Moscow in December, 1979. The Congress was to be held in the Moscow State University which had many suitable lecture and other rooms which were inspected by the SPC. At the final dinner of the SPC meeting, Professor Aschoff made the point that the language of international science was now English and that if the Soviet hosts were to participate in international science, they had three years before the Congress to learn it; many took his advice, which greatly enhanced the exchange of ideas between Eastern and Western ornithologists.

President von Haartman interacted closely with the Soviet organizers in planning for the Congress and made at least one additional trip to Moscow in connection with this work. In the fall of 1981, Professor D. Farner spent two weeks in Moscow and Professor W. Bock two months to assist in preparations for the Congress, partly to arrange details of meetings, but mainly to assist in editing the abstracts. Bock spent the second part of his time working in the anatomical laboratory of Professor F. Ya. Dzerzhinsky in Moscow State University, and also attended a meeting of Socialistic Morphologists. On his homeward journey, he stopped in Helsinki, Finland and briefed President von Haartman on the progress of the Congress. Upon being informed of the recent death of Dr. E. Eisenmann (USA, and chair of the SCON), von Haartman asked Bock if he would take over the chair of the Standing Committee on Ornithological Nomenclature which he accepted.

The 18th Congress opened with a greeting by President von Haartman in a dazzling series of languages. The scientific program of the 18th Congress followed that of the 17th closely. In addition to the Presidential Address, there were five plenary lectures, 17 morning symposia, 24 afternoon symposia, poster papers and Round Table Discussions. An important feature of the scientific program was the large number of contributing Soviet and Eastern block ornithologists, providing a good insight into the diversity and depth of research in avian biology in those countries.

Papers appeared in the Proceedings of the 18th Congress as follows: Official Reports (prepared by Walter Bock), the plenary lectures, full papers of morning symposia, abstracts of afternoon symposia, abstracts of most poster papers, some full poster presentations, and reports of RTDs (only a few were received by the editors of the Proceedings). It is interesting that rather long abstracts of a poster and of an RTD from one of the editors appeared in the Proceedings. In its report, the SCON stated that it would begin a project on the history of avian family-group

names, an essential task before nomenclatural decisions could be reached on these names as required by the current Code of Zoological Nomenclature; this rather large project would be accomplished in 1994 (see the 21st Congress, 1994). Unfortunately the Proceedings do not include any details of the large series of tours held on the congress free-day or of the many outstanding post-congress excursions to diverse parts of the Soviet Union.

With extensive changes to the IOC Statutes and By-laws from the 17th Congress, a number of questions were raised at both the meetings of the PEC and the IOC to clarify their implications. Most importantly, it was emphasized that former Presidents are now permanent members of the IOC and that emeritus members of the IOC (those over 65 years of age) are not counted toward the specified total number of members or as representatives of their home countries in the IOC. In either case, additional members can be elected. Further, it was suggested that former Secretaries-General be made permanent members of the IOC so that their most useful knowledge about the organizing and running congresses could be tapped. A small committee was established to examine these and other matters arising from the new Statutes, and to consider any required resolutions to present to the IOC for adoption. However, no resolutions were presented to the IOC for action at its second meeting, and a motion was put forward to ask the committee of Professors von Haartman, Farner and Ilyichev to approve the resolutions. It is not clear from the Congress Proceedings whether this action was undertaken.

Several important amendments to the By-laws were passed at IOC meetings during the Congress, but were not noted in the Official Report or elsewhere in the Proceedings. These changes can be found by comparing the Statutes and By-laws published in the Proceedings of the 17th Congress with those published in the 19th Congress; the Statutes and By-laws were not included in the Proceedings of the 18th Congress. One change was the addition of a Vice-President to take over the reins of the IOC should the elected President become unable to continue in his/her duties. Another was a change in Article I of the By-laws in which was added the sentence: "Members of the IOC must be residents of the country that they represent." (Proceedings 19th Congress, p.88). These major omissions in official reports of the IOC and its PEC, often the result of abridged accounts of what happened at their meetings at congresses, demonstrated clearly the need for an additional officer of the IOC, namely a Permanent Secretary. This issue was resolved at the 19th Congress.

Attention was now given to the election of new

members of the IOC. The procedure had not been worked out carefully, and only one person was nominated by the PEC. President von Haartman proposed that the IOC form a committee to nominate and then elect new members. The result could best be described as semi-controlled chaos; Professor Farner became discouraged and departed in protest. At this point, President von Haartman blocked the door with a chair to prevent other IOC members from leaving. Individual ornithologists were quickly nominated one after the other with no additional information than their name and country of residence. It quickly became clear that a recording secretary was needed, and President von Haartman asked Walter Bock to undertake this task. A long list of nominees was put together and they were promptly elected as new members. I was then asked to contact these new members after the Congress (some of whom I did not know), informing them of their election. My suspicion is that at least one person who was not on the list was so informed because of similarity of names. Nor was it certain whether more new members of the IOC were elected than permitted under the Statutes and By-Laws. But these proved minor issues, and the IOC continued to survive and function properly.

Approval was given for the establishment of a permanent archive for the IOC and a committee was established to look into this matter. Agreement was reached with the Smithsonian Archive in Washington, DC, as storage venue, with the papers signed by Donald S. Farner, Henri Ouellet and Walter J. Bock for the IOC (Proceedings, XIXth Congress, p. 60). But few members of the IOC have yet forwarded their papers to it. Members are urged to do so wherever possible.

A discussion on the nature of the congress scientific program was held because of concern that ornithologists did not have time for individual discussions and that talks presented at the congresses, especially in the symposia, tended to deal with matters of past importance rather than new discoveries and ideas of future significance. The last point is indeed real. For most ornithologists after World War II, speed of publication and a broad dissemination of new findings and ideas are of importance, and these needs are not guaranteed by publication in congress proceedings. Most members did agree that the combination of the plenary lectures and symposia conveying ideas from specialized areas of avian biology to the general ornithologist, individual contributions in the form of poster or other papers providing a way for any ornithologist to convey his/her work to the international community, and the RTD's as a forum for detailed discussion among specialists in any field, provide a sound and appropriate format for the scientific pro-

gram of ornithological congresses. Attention has also to be given to the issue of providing sufficient time during the congress week for contact between individual ornithologists.

Concern was also raised on the matter of invitations for future congresses, and whether the IOC should act on any other than those submitted for an ensuing congress. It was pointed out that the work to prepare a congress invitation took several years, and hence it was useful for ornithologists in different countries to propose intended invitations as early as possible, e. g., work for an invitation for the 19th Congress should start before the end of the 17th Congress, even though the final invitation is not made until the 18th Congress. The IOC then voted to accept the invitation from Canada for the 19th Congress, 1986, in Ottawa, to complete the first 100 years of international ornithological congresses. Professor Klaus Immelmann (Germany) was elected President, with Dr. Henri Ouellet (Canada) appointed the Secretary-General and Professor J. Ashoff serving as the designated replacement President for the 19th Congress.

The 18th Congress was a great success for a number of reasons, foremost among which was the getting together of ornithologists from two estranged blocks of nations to interact as is proper in international science. To my knowledge, no ornithologist was denied a visa to attend the Congress, though some were delivered at the last moment in line with the ways that some governments interacted during the cold war. The 18th was also the first congress to operate under the effective new Statutes adopted at the 17th Congress in Berlin—a tribute to the work and vision of Professor Farner.

## 15 Back to the New World—the 19th Congress, Ottawa, 22 – 29 June 1986

Under the direction of an efficient Secretary-General, Henri Ouellet, the Canadians started immediately on the organization of the 19th Congress, establishing a series of committees to deal with all aspects of the meeting. President Klaus Immelmann appointed the Scientific Program Committee, with Professor Bruce Falls (Canada) as its chair. The Canada jay *Perisoreus canadensis* was, not unexpectedly, chosen as the Congress emblem. Planning for the congress went well, all committees meshing properly in doing their tasks and reporting to the two meetings of the entire Local Committee held in Ottawa. The SPC met once in Ottawa, in October 1983, with its North American members also attending later meetings of the Local Committee. The 19th Congress met in the newly constructed Ottawa Congress Centre which has excellent facilities for a

large international meeting, with numerous dining and other facilities both in the building and nearby. Day to day planning and running of the 19th Congress were contracted out to Lemmex and Associates—professional conference organizers; this was the first ornithological congress in which such arrangements were made and it set the pattern for the future.

The 19th Congress was larger than any of the previous congresses, with a total of 1 338 members representing 65 countries (1 154 full members, of which 68 did not attend). The scientific program comprised the Presidential Address, a lecture by the Secretary-General on the history of Canadian ornithology, five plenary papers, 50 symposia, 150 oral and 380 poster presentations, and 43 RTD and other special interest meetings. In recognition of the 100 anniversary of the founding of the international ornithological congresses in Vienna in 1884, a display was prepared by Herbert Schifter (Austria) and Walter Bock (USA) using materials from the archives in Vienna. Professor Charles Sibley presented a special exhibit of his findings on interrelationships of birds based on his studies of DNA-DNA annealing along the side of the large room of posters and exhibits. His results were shown on a 10 meter long, 1 meter wide strip of paper that was labeled by one congress member as “the tapestry.” Although it cannot be confirmed, it was reported that Professor Sibley spent almost his entire time at the Congress sitting next to his tapestry, ready to speak to every one wishing to discuss diverse aspects of avian relationship. The film program contained 85 films, some of which were shown more than once. A total of 13 pre- and post-congress excursions were held, reaching almost all corners of Canada, together with early morning bird walks and a series of tours on the congress free-day of Thursday, 16 June. Members went home exhausted.

Unfortunately, the Official Report of the Congress was customarily brief, so that considerable reading between the lines was necessary to tease out its events. Two excellent invitations for the 20th Congress in 1990 were received, one from Japan and the other from New Zealand. Dr. H. Morioka, in presenting the Japanese invitation, informed the delegates that all languages would be acceptable at a congress held in Japan—Japanese English, German English, French English, and even American and Australian English. After their presentation and discussion, the IOC voted to accept the New Zealand invitation for the next congress in Christchurch. Professor Charles G. Sibley (USA) was elected President and Professor Jan K. Pinowski (Poland) Vice President. Further, Dr. N. K. Kuroda (Japan) was elected as the Honorary President and Professor Walter J. Bock (USA) as the first Permanent Secretary. Three

of these positions resulted from changes to the Statutes proposed by an Advisory Committee on Statutes (Proceedings, p. 59). First, it was decided at the Moscow Congress that it was advisable to have a position of Vice-President of the IOC, and hence of the congress, who could serve as President should the elected President not be able to continue in office; accordingly, that position was added to the Statutes. Secondly, although the Statutes did not prohibit the election or nomination of honorary officers for a congress, such action was agreed to in principle although has not been so specified in the Statutes and By-Laws. From the 20th congress onward, an Honorary President was elected, generally to recognize a senior ornithologist.

Still more importantly, it had become clear to President Immelmann and Secretary-General Ouellet that two major difficulties confronted the organization of the IOC and its congresses. One involved the responsibilities of the Secretary-General. These had become too heavy for any one person, diverting the Secretary-General from his/her primary obligations in organizing and running the congress. One Secretary-General, Niko Tinbergen, had already broken down under the strain after the 1966 Congress at Oxford. For modern congresses, such tasks required the full attention of the Secretary-General, preventing him/her from devoting the time needed to record the discussions and decisions of the PEC and the IOC, and to report these fully in congress proceedings. The task of securing invitations for future congresses had also become a major task both for ornithological groups interested in hosting a congress and for the IOC because the requirements for preparing an invitation had increased in complexity.

The other major difficulty concerned long-term “institutional memory”, or, more importantly, the lack of it among the officers of the IOC. The President and Secretary-General of any congress serve only one term. Even their additional service, as past officers, in the PEC for an additional term and the general service of elected PEC members for two terms, members of the PEC did not provide sufficient institutional memory. Immelmann and Ouellet felt the need for smoother operational continuation, and hence a better institutional memory. So they recommended a new position, that of a Permanent Secretary whose duties were to run the IOC and PEC both at and between congresses, and to plan for future congresses, leaving the Secretary-General free to focus unfettered on running the congress current. This approach was accepted unanimously by members of the IOC of the 19th Congress, and Professor Walter Bock, who had, in effect, served in this capacity at the 18th Congress, was elected as the first Permanent

Secretary and charged with providing the necessary modifications to the Statutes for consideration at the 20th Congress in 1990.

An amendment to the Statutes was proposed and passed by the IOC that new members of the IOC must have attended at least one ornithological congress to be eligible, even if it was the one at which they were elected. Unfortunately this change was not recorded in the Congress Proceedings, again demonstrating the need for the new position of Permanent Secretary to oversee such matters. The omission was finally noted at the 22nd Congress in Durban and re-adopted there. The number of elected members of the IOC was increased to 120, and five new members were elected (Proceedings, p. 59). As well, a new Standing Committee on Applied Ornithology was appointed (Proceedings, p. 60) under the co-chairs of Professor V. Ilyichev (Soviet Union) and Dr. P. Peterson (USA).

The 19th Congress ended with a formal closing Ceremony in the late afternoon of Saturday, 28 June, possibly the first post-World War II congress to have a definite closing, despite its omission from the daily printed program; all subsequent congresses included a formal closing Ceremony. The 20th Congress in New Zealand was announced at the same time, as well as the new officers and members of the IOC and the PEC. The 19th Congress was clearly the largest International Ornithological Congress to date in terms of members, number of presentations and size of its Proceedings. Moreover, it was an exceedingly well organized and excellently run congress, setting the standard for the future. Unfortunately, President Klaus Immelmann died just over a year after closing a congress over which he had presided so well; a memorial is included in the Proceedings (pp. 7–9).

Following the 19th Congress, the Permanent Secretary prepared a many-paged set of instructions for the preparation of invitations and for organizing future congresses. These instructions are available from the current Permanent Secretary to any group of ornithologists interested in hosting a congress.

## 16 Back to the Antipodes—the 20th Congress, Christchurch, 2–9 December 1990

Immediately following the close of the 19th Congress, President Charles G. Sibley (USA) appointed Dr. Ben Bell (New Zealand) as the Secretary-General of the 20th Congress who then arranged the membership of the necessary New Zealand Organizing Committee and its subcommittees. The yellow-eyed penguin *Megadyptes antipodes* was chosen as the Congress emblem, representative of the “South-

ern Perspective” theme for the 20th Congress. As for the 19th Congress, organizational details were arranged by a professional conference organizer, Conference Makers Limited. Sibley also appointed Professor Peter Berthold (Germany) as chair of the Scientific Program Committee, despite a major protest from the New Zealanders who wanted a New Zealand ornithologist to chair it. This matter was straightened out by letters to the New Zealand organizers from Professors Donald Farner and Walter Bock at the request of President Sibley. Over the next four years, the New Zealand Organizing Committee met about 80 times, sending all reports to me and I assume also to President Sibley; one wonders what they discussed during so many meetings. The SPC met in November, 1987 in Tiburon, California, the home of Professor Sibley. This had serious disadvantages because the SPC was unable to see the actual congress site, depriving it of an appreciation of the arrangement of the meeting rooms which is most useful in formulating the scientific program of a congress, such as appreciating the arrangement of doors and seating in each room and knowing the time required to move from one session to another, etc. At its meeting, the SPC decided on a program of four plenary lectures in addition to the Presidential Address, a New Zealand evening with two lectures, 48 symposia, and contributions in the form of oral (276) and poster papers (233) papers, as well as round table discussions (31), special interest groups (10), and films (39). President Sibley was able to visit New Zealand prior to the Congress and discuss progress and arrangements with the Local Committee.

With the agreement of the Permanent Executive Committee, President Sibley appointed Professor Hsu (= Xu) Wei-Shu (China) and Professor Helmut Sick (Brazil) as Honorary Vice-Presidents of the 20th Congress.

The 20th Congress was part of New Zealand's 150th Year Celebration of the founding of their modern government, and was held under the banner of the “The World of Birds—a Southern Perspective”. It also included the 20th World Conference of the ICBP in Hamilton, the Pacific Festival of International Nature Films in Dunedin, and the BirdPex '90 Stamp Exhibition in Christchurch. The Congress opened at the Christchurch Town Hall with a traditional Maori challenge involving a Maori warrior at the head of the procession of the official party, walking backwards and jabbing at President Sibley with a spear, cheered on by the congress members. Set in a large and attractive parkland on the outskirts of Christchurch, the campus of the University of Canterbury was the venue for all other congress activities, the first time that a university site had been used

since the 16th Congress in 1974, and possibly the last. A major problem in universities is the lack of large lecture auditoriums, essential for plenary lectures for large international congresses. The solution used in Christchurch, that of dividing the audience into two halls, the second of which was fed by a video system, did not work well. Another problem stems from the distances between lecture rooms in universities; such distances are usually between buildings, and even if short, still cause problems for congress members wishing to change sessions, as happened at the Christchurch Congress.

The Christchurch Congress was large, attended by 883 regular members, 135 accompanying persons, and 285 student members and staff volunteers. Unfortunately New Zealand did not abide with the strict regulations of the International Union of Biological Sciences on freedom of movement of scientists to international congresses under the auspices of the I-UBS: no ornithologists carrying South African passports were issued visas to attend the 20th Congress.

Diverse tours on the mid-congress free day converged at the Mount Hutt Station where an excellent High Country Fair was held, followed by a barbecue. A comprehensive series of pre- and post-congress excursions visited a broad range of New Zealand habitats, allowing congress members to see a great diversity of the unique New Zealand avifauna and its environment. The 20th Congress had also planned a unique post-congress sub-Antarctic cruise on the new M. V. Frontier Spirit. Unfortunately this ship was damaged in a November cyclone off Fiji, and the cruise had to be cancelled. In its place, however, 77 congress members were able to arrange a substitute cruise on the M. V. World Discovery, and this was most successful.

The PEC met five times during the Congress, largely to deal with modifications to the Statutes concerning the establishment of the position of Permanent Secretary. In the end, the changes as proposed by Walter Bock were accepted and forwarded to the IOC where they were adopted. Basically, the duties of the Secretary-General are concerned with the running congress for which he/she is appointed by the President, while those of the Permanent Secretary are concerned with the operation of the IOC and interacting with prospective hosts in the preparation of invitations for future congresses. The Secretaries-General and Permanent Secretaries are both permanent members of the IOC. In addition, provision was made for the appointment of Honorary Presidents and Vice-Presidents who are *ex officio* members of the IOC during their term of office. It was also proposed that the membership of the IOC be raised to 140, and that for the Permanent Executive to ten; with the 5 *ex*

*officio* members, the total membership of the PEC now became 15. Senior members of the IOC were no longer subject to Art II. 4 of the Statutes (= automatic resignation from the IOC following absence from two successive congresses).

These changes in the Statutes and the By-Laws were adopted at the IOC meeting of the 20th Congress. Further, the IOC voted to accept the invitation from Austria to hold the 21st Congress in Vienna in 1994. Dr. Christopher M. Perrins (United Kingdom) was elected President of the 21st Congress, Svein Haftorn (Sweden) as Vice-President, Walter J. Bock as Permanent Secretary and Karel H. Voous (The Netherlands) as Honorary President. Dr. John Dittami (Austria) was appointed by President Perrins as its Secretary-General. Three members of the PEC were re-elected and seven new members elected (Proceedings, pp. 69–70), and a large slate of 62 new members and 3 re-elected members of the IOC were proposed by the Nominating Committee (Proceedings, pp. 69–70). Resolutions were passed concerning ornithological nomenclature, the need for scientific posts in the Sub-department of Ornithology at the British Museum (Natural History), and possibly serious detrimental effects on migrating birds by construction of the large Voice of America relay station in the Aravah Valley, Israel. In response to the report of the RTD on Standardization of English Bird Names, the IOC established an international committee under the chair of Professor B. Monroe to develop such a list. An international group to standardize French bird names was also established under the chair of Dr. H. Ouellet.

In conclusion, the IOC gave a strong vote of appreciation to all persons involved in the successful 20th Congress in Christchurch.

## 17 Back to our roots—the 21st Congress, Vienna, 20–25 August 1994

Ideas for a second congress in Vienna had been in the air before the 1986 Congress and came to fruition with the acceptance of an invitation from Austria at the Christchurch Congress. Several early discussions were held between Walter Bock and various Austrian ornithologists for preparing the invitation. He did not meet with the future Secretary-General John Dittami then because on the one occasion that Bock was in Vienna just prior to 1990, Dittami was brutally mugged the night before at the railroad station in the small suburban town outside Vienna where he lived.

The emblem for the 21st Congress was the grey-lag goose *Anser anser*, the bird much studied by Konrad Lorenz. At the suggestion of Professor Dittami, President Perrins appointed Professor John C.

Wingfield (USA) as chair of the 12 member Scientific Program Committee. The SPC met in late August of 1992 in a small resort hotel west of Vienna and agreed on the usual program of plenary lectures, symposia (52), poster papers (over 500) and round table discussions. One notable change was an increase in the number of plenary lectures, including the Presidential Address, to ten to enable a better coverage of the ever-widening spectrum of ornithological research.

The increased number of plenary lectures at the 21st Congress proved a great success, but their consecutive arrangement, one after the other at the start of the morning session, was heavy going. Many congress members favored one plenary lecture at the beginning of the morning and one at beginning of the afternoon, as was to become standard practice at subsequent congresses. Several special evening lectures were also organized by the Secretary-General. Unfortunately there was no film program. Moreover, because the congress program was scheduled over only six days, the traditional mid-congress free day was not held either.

Although the original site suggested for the Congress was the new Vienna Convention Center, which has excellent facilities, it was rather isolated, located well away from the center of Vienna and most hotels. Subsequently, the convention facility at the Hofburg in the city center was chosen, a much more convenient site in spite of its poorer appointments. Air conditioning was non-existent and, as it turned out, meeting rooms became stifling during a heat wave in Vienna at the time of the Congress. President Perrins was able to visit Vienna to inspect the convention facilities at the Hofburg in the early fall of 1992 after the suggestion to change venues had been made by Secretary-General Dittami. Because of continuing organizational problems, a special two-day meeting was held at Oxford, U. K. in November 1993, with Perrins, Bock, Dittami and Dr. Hans. Winkler present to work them out.

The 21st Congress was attended by over 1 300 members from 70 countries, a huge increase from the 1st Congress in 1884. Its opening in the Arcades of the University was very pleasant, most informal and was followed by a buffet supper. Notable among the members were Wilhelm Meise (Germany), Max Nicholson (UK) and Ernst Mayr (USA) whose attendance at ornithological congresses dated back to the late 1920's or early 1930's, before most members of the 21st Congress were born. Professor Mayr was awarded an honorary doctoral degree from the University of Vienna and the Godman-Salvin Medal from the British Ornithologists' Union during the Congress. It should also be noted that immediately

prior to the Congress, he was chosen as the winner of the 1994 International Prize for Biology presented by the Japan Society for the Promotion of Science; it was awarded to him by the Emperor of Japan in November, 1994.

The ICBP held its World Conference immediately prior to the Congress, and every effort was made at the Congress to accommodate ICBP attendees as well. Plenary lectures and symposia of interest to members of the ICBP were scheduled to take place on a single day, but it is not clear whether this plan enticed many ICBP members to attend. Because of the extensive re-organization of the ICBP after 1994, and its decision to terminate its World Conferences, this was the last time that these two groups met in conjunction, the end of a tradition that starting at the first congress after WW II.

Meetings of the PEC and the IOC covered considerable ground efficiently (Proceedings, pp. A130 – 133). Finances had become a major problem, both for congress organization and for travel for many ornithologists from poorer countries. As one solution for the latter, it was agreed that the IOC could send to all ornithologists wishing to attend congresses a letter of invitation which could then be used to support applications for funds from their home country. Another related problem was the publication of the Proceedings, which had grown greatly in size such that its costs now constituted a sizeable part of the registration fee. Shortage of funds had already produced a skimmed volume of abstracts, in which text was simply guillotined off in a make-shift page trimming process. Other significant costs incorporated into the registration fee had come from the hiring of convention centers and of travel/convention companies to assist in the running of congresses now that the congresses had become so large. The days of undertaking congresses with only the help of the congress committees and a corps of volunteers, as happened before 1986, had passed. International ornithological congresses have become increasingly successful and well attended; with such success and numbers of congress members have come increased organizational problems and costs.

A further nagging problem concerned the composition of the IOC. Its representation by country, according to the Statutes, should be in proportion to the relative size of the country's ornithological activity. Assessment of the amount of ornithological working different countries had never been attempted, and still has not been done. Concern was also expressed about increasing competition from the growing number of regional ornithological congresses and special interest groups.

The reports of the Standing Committees on Or-

nithological Nomenclature, Seabird Research and Applied Ornithology were submitted to the IOC (Proceedings, pp. 133 – 141). The SCON announced that the major project on avian family-group names was finally completed (Bock, 1994), a project that dated back to 1962. At the 18th Congress in 1982, the SCON stated that it would tackle this major nomenclature project for birds. Its completion provides the first thorough analysis of the history and nomenclature of family-group names for any major group of animals. The death of Burt Monroe brought the complicated project for a standardized list of English names for birds to a temporary halt. It was restarted soon after the Vienna Congress when Dr. Frank Gill (USA) agreed to serve as the chair of the English Bird Name Committee, and the project is now close to completion.

Following the recommendations of the PEC, the IOC voted to accept an invitation from South Africa for the 22nd Congress in 1998 and elected Peter Berthold (Germany) as its President, Janet Kear (United Kingdom) as Vice-President, Walter Bock as Permanent Secretary and Cheng Tso-Hsin (China) as Honorary President. Members of the PEC and new members of the IOC were also elected. Dr. Aldo Berruti (South Africa) was appointed by President-elect Berthold as the Secretary-General for the 22nd Congress.

After five days of clear hot weather, a strong cold front went through Vienna just after the formal close of the Congress and immediately before the beginning of the final reception and evening banquet at the Vienna Zoo in Schönbrunn—an event that will be long remembered by all congress members attending. But I cannot provide any first hand comment because I, together with Hans Winkler and our wives, left the zoo early for a quiet dinner in the city. Although the event was carefully planned, the first mistake was to separate congress members into different parts of the zoo as noted carefully on their tickets. Then came the rain and wind, drenching uncovered seating areas and blowing away table ware. There was no plan B. What followed was a metaphor for Robbie Burns' line: "the best laid plans o' mice and men gang aft a-gley." I only learned later of the intermittent loss of electricity and the uneven distribution of food and people because many members had become confused about the seating areas stated on their tickets. Finally, the coup de grâce was delivered by a locked exit gate, preventing members from leaving the zoo at the end of the banquet. The crowd milled around it in bemused frustration. Directions and zoo attendants were conspicuous by their absence. Some of the younger members, it was reported to me, attempted to get over the gate by climbing the fence of the enclosure

next to it without realizing that the enclosure was the zoo's lion cage. Fortunately, there were no serious accidents, and a small alternative exit was eventually found, allowing the crowd to leave and return safely to their hotels.

Funds were not available to publish a Congress Proceedings of more than the available plenary lectures and the Official Report of the Congress. The 21st Congress Proceedings were published by the BOU in *The Ibis*, volume 138 (#1), 1996 and then reissued as an undated separate, *Acta XXI Congressus Internationalis Ornithologici*, which will cause some bibliographic problems, even though the pagination of the plenary lectures in the two publications is the same; the second Acta contains additional pages in the back of the volume containing the official reports of the congress. The difficulties confronting the publishing of congress proceedings came to a head at Vienna; yet it took only the next Congress in Durban to reach a reasonable solution.

## 18 South again—the 22nd Congress, Durban, 16–22 August 1998

Interests by South African ornithologists to host an international ornithological congress had been long standing, starting formally with an invitation at the 11th Basel Congress, 1954 for the 12th Congress in 1958. Unfortunately, the world economy could not support an ornithological congress outside of Europe then. Records in the proceedings of the 12th Congress do not indicate whether there was a repeat invitation from South Africa, but it is clear that when the decision was taken to set the venue of the 13th Congress, 1962 outside of Europe, it was necessary to honor the vote of the 9th Congress, 1938 to hold the 10th congress in the USA, then scheduled for 1942. It should be mentioned that the first invitation for an ornithological congress from Africa came from Tunis at the 6th Congress, 1926 for the next one in 1930. After 1962, the apartheid policy of the government of South Africa largely precluded hosting a congress in this interesting ornithological region, with its long-active group of avian biologists.

Occasional discussions had been held between Walter Bock and Dr. Tim Crowe (Cape Town: South Africa) on the possibilities of a South African congress, and these intensified in 1991 as soon as it became clear that South Africa was moving to a new government based on fully democratic elections. I believed that the congress would be held in Cape Town, the major center of ornithological activities in South Africa. But in November 1992, Crowe suggested Durban to me and recommended Dr. Aldo Berruti as Secretary-General. After the necessary introductions, correspondence started between Berruti and Bock

which resulted in an invitation for Bock to visit Durban in early May 1993. I was able to meet and talk with Durban city officials, members of Durban's new convention center, representatives of the African National Congress and the Inkata Freedom Party, and officers of the Southern African Ornithological Society. The result of this trip was a formal invitation presented to the IOC at the 21st Congress by Aldo Berruti on behalf of southern African (not just South African) ornithologists to host the 22nd Congress in Durban in August 1998. This invitation was accepted with enthusiasm.

The symbol for the 22nd Congress was Gurney's sugarbird *Promerops gurneyi*, a most appropriate choice of an avian group endemic to southern Africa. After President Berthold had appointed Dr. Berruti as Secretary-General and the necessary National and Local Committees were established, he appointed the Scientific Program Committee under the chair of Dr. Lukas Jenni (Switzerland). This committee met in early October 1995 in one of the lovely national parks in Kwazulu-Natal Province after inspecting the convention site and hotels in Durban. The SPC decided to maintain the system of 10 plenary lectures, but arranged them so that a plenary lecture opened each morning and afternoon session of the five working days of the Congress. This system worked very well, the plenary lectures serving as inducements for members to be on time for both morning and afternoon sessions. In addition, there were 10 symposia a day, five in the morning and five in the afternoon with two South African Lectures in the evening of the first working day. At the 1995 meeting of the SPC, 45 symposia were accepted with five symposia slots left open for later suggestions; a total of 51 symposia were presented in the end. Contributed papers were divided into oral and poster papers, those for the 120 oral slots (in 15 sessions) being selected by members of the SPC on the request of the speaker. As for earlier congresses, RTDs were not to be organized as symposia. Also as in earlier congresses, any one person could only convene or speak in one symposium; only one exception had to be made to this rule. All abstracts were to be submitted electronically, as was most of the registration. The change to the Internet medium saved a great deal of time and expense for this and successive congresses.

The problem of publishing congress proceedings was then considered, although it was not within the responsibility of the SPC. The singular difficulty was the cost of publication of the full symposia papers, in contrast to the alternative of publishing no more than a longish abstract of each. Eventually a proposal was made to and accepted by the South African Local Committee to publish the entire congress proceedings



as a CD-ROM disk which included the reports of the congress, the full texts of the plenary lectures and of the symposium papers, the abstracts of the contributed papers and reports of the RTD's. Subsequently the decision was made to publish the plenary lectures in an issue of *The Ostrich* as well. The entire Congress Proceedings eventually ran to the equivalent of 3 672 printed pages in the *The Ostrich* format, the symposium papers themselves occupying 3 164 pages. Without a question, the Proceedings of the Durban Congress are the largest of all congresses so far, a result made possible only with electronic publishing in CD-ROM format.

Announcements of the Congress were made in the usual way by placing advertisements in many leading ornithological journals, but a congress home page was also established on the World Wide Web. Registration and most correspondence for the Congress, including submission of abstracts and use of credit cards for payments, was carried out almost entirely electronically, saving a great deal in postage and speeding up correspondence time. President Berthold was able to visit Durban the year before the Congress to further inspect the site and to discuss arrangements with Secretary-General Berruti and members of the Local Committee. The newly constructed International Congress Center in Durban and its proximity to hotels, as well as the overall planning and running of the Congress, were outstanding and on par with the excellent facilities and organization at the 19th Congress in Ottawa. Most interesting, as well as a complete surprise to members, was a barrier of concrete road traffic dividers placed around the Congress Center the day after the Congress opened, in the direct path of most members walking to the meeting and over which they had to climb to reach and leave the Congress Center. The concrete dividers, it transpired, were not installed to protect the good citizens of Durban from the assembled ornithologists, but for a major meeting of Non-aligned Nations which was to take place at the Congress Center the following week.

One major and unexpected problem was created by the large number of persons who submitted an abstract early without further registering or attending the Congress. Whether this action was intentional, thereby providing the person with another title in their bibliography, or caused by shortage of funding to attend the Congress, could not be determined. As a result, many empty poster boards stood empty, at a major cost to the Local Committee for their rent and to the chagrin of congress members.

The attendance at the Durban Congress totaled 1 083 registered members, far fewer than had been estimated and barely two-thirds of the rather conservative estimate of full members by Berruti and Bock

Clearly finances had been a major factor, even in the first-world countries. Even more disappointing was the dearth of African ornithologists attending the Congress. The small number of members placed serious strains on the finances of the 22nd Congress, because every congress has a fixed minimum cost regardless of the number of attending members. This raises a dilemma for international ornithological congresses. A survey of attendance records shows that congresses held outside of Europe and North America have been much smaller than those within such hubs of ornithological activity. Yet, if the ornithological congresses are to be truly international, they must meet in all parts of the world.

A British Ornithologists' Union day took place on Sunday, 16 August prior to the Welcoming Ceremony, with special lectures on ornithology in Africa. Although no further details of this satellite meeting are given in the Proceedings, an account was provided by Bucknell (1999). The meeting of the World Working Group on Birds of Prey and Owls (headed by Dr. B.-U. Meyburg, Germany) took place in Midrand, South Africa immediately before the Congress, but independently. Unfortunately few members of this working group attended the Congress.

The Welcoming Ceremony took place in the evening of Sunday, 16 August, followed by a reception. An account of the scientific program of the Congress can be obtained by examining the full Proceedings which lists all of the papers and provides the abstracts for the contributed papers and the Round Table Discussions, as well as references to all of the abstracts which were published in *The Ostrich*, Vol. 69, 1998. Following the Closing Session in the late afternoon on Saturday, 22 August, the congress banquet was held in a large tent attached to the back of the Congress Centre. After a week of excellent weather for the congress, there was a heavy down-pour during the banquet, fulfilling the Congress slogan: "Making rain for African ornithology." The tent held except in a couple of places where different segments overlapped and allowed water to pour in without, fortunately, dampening anyone or their spirits.

A full set of pre-and post-congress tours had been arranged, as well as excursions on the mid-congress free day, Thursday, 20 August. Most of the interesting avifaunal areas of southern Africa were covered. Unfortunately no reports of the tours were included in the Proceedings.

Much business was completed at the meetings of the PEC and the IOC which are best treated together. Nominating Committees were established for candidates for offices and membership of the PEC and

IOC Although President Berthold had communicated with all members of the PEC and obtained full agreement on the slate of candidates for the offices, a new candidate was introduced without any warning at the first meeting of the PEC. This unexpected nomination led to considerable argument which became quite heated at times, and led to a long extra meeting of the PEC. The final vote supported the original slate that had been worked out prior to the Congress, and this was then passed by the vote of the IOC. It was decided that in the future a nominating committee for the officers be established under the chair of the immediate Past-President. A nominating committee had often been appointed for ensuing congresses, but not always with the immediate Past-President as the chair. Voting for the officers of the 23rd Congress resulted in the election of Walter J. Bock (USA) as President, Jacques Blondel (France) as Vice-President, Dominique G. Homberger (USA) as Permanent Secretary, and Ernst Sutter (Switzerland) as Honorary President.

Two excellent invitations for the 2002 congress were received and presented to the PEC, one from Israel and one from China. Professor Bock had visited both sites and discussed each invitation with the ornithologists from the prospective host countries. After a full review of the two invitations, the PEC accepted and forwarded both to the IOC, asked the ornithologists from both host countries to present their invitation there, and opened the floor for a full evaluation. After long discussion, the vote was strongly in favor of China. So the first congress in Asia would begin the third century of ornithological congresses. Subsequently Professor Xu Wei-Shu (China) was appointed as Secretary-General for the 23rd Congress. Not unexpectedly, the Israeli members of the IOC were most disappointed that their invitation lost. In the years between 1998 and 2002, unfortunately, the security situation in Israel had degenerated so much that in July 2002, shortly before the opening of the 23rd Congress, Yossi Leshem of the Israeli delegation sent President Bock a message expressing relief that Israel was not hosting the 23rd Congress and wishing the Beijing Congress great success.

Nominations for elected members of the PEC were formulated at the meeting of the PEC, as well as a slate of nominations for new members of the IOC prepared by a committee headed by Professor Cynthia Carey (USA). Both slates were presented to the IOC which approved them with one deletion. During the PEC's discussion of the slate of IOC members it was realized that the amendment to the Statutes passed at the 19th Congress, which required new members of the IOC to have attended at least one congress, had not been included in the published Statutes or men-

tioned in the Proceedings of that Congress. Hence this amendment was proposed once more by the PEC and passed by the IOC [see Art. II (3)]. In addition, the size of the IOC was increased to 200 national representatives.

A number of organizational matters of congresses, including the work of the SPC, were discussed on the basis of a full report on the SPC submitted by its Chair, Lukas Jenni. It was recommended that, as far as possible, all correspondence for future congresses should be electronic. Using this medium, meetings of the SPC could be delayed to within two years of congresses instead of the usual three. A fee should also be charged for the submission of abstracts to cover the cost of publishing the abstract and presenting the contribution at the congress; the submission fee would be subtracted from the congress fee when the person registered for the congress.

Reports of the Standing Committees on Ornithological Nomenclature and Applied Ornithology were submitted. Further, the IOC established three new Standing Committees on Avian Anatomical Nomenclature, Raptor Studies and Ringing. A Standing Committee for Ringing of the IOC had been established at the 17th Congress, Berlin, 1978, but this committee apparently never met and was defunct. The chairs of the existing and the new Standing Committees were requested to submit the lists of their members to Bock for appointment in the 1998–2002 period. Unfortunately most of these committees, with the notable exception of the SCON, were inactive through that time.

Financing remained a continuing problem for the IOC, affecting start-up funds for congress organization and funds to allow ornithologists from developing countries to attend congresses. The IOC is a tax-free organization in that it does not use operating funds. The work of officers in inter-congress periods had always been supported by the officers themselves, a situation that cannot be depended upon in the future. Additional costs were being incurred as well, such as the maintaining of a WWW home page, now essential for the work both the IOC and congresses. Moreover, the Local Committee for each congress needs start-up funds, much of it required to cover expenses for the meeting of the SPC which takes place before any registration fees are received. To date, the raising of such funds has been the responsibility of Local Committees of host countries, placing an unfair demand on them. Perhaps the greatest effort to raise funds for supporting ornithologists to attend a congress was made by Canada for the 19th Congress in Ottawa. Various Canadian ornithologists went all out to obtain support; but such activity cannot be expected for all countries or every time. Complicating

understanding of these financial matters is that, aside from the report of the finances of the 13th Congress in Ithaca (which was included in the financial report of the AOU for that year), almost nothing is known about the actual finances of congresses, either the income or the costs; to my knowledge no detailed financial report has been published in the proceedings for any congress. As a result, President Bock arranged to appoint a committee that would assess all aspects of these questions and report to the 23rd Congress.

The 22nd Congress was the first since World War II at which the ICBP (now BirdLife International) did not hold a conjunctive World Conference, its demise drawing attention to the need for increased attention on scientific aspects of avian conservation at international ornithological congresses. The related questions of holding other international meetings independently of international ornithological congresses, and of satellite meetings in association with them, were examined. Accordingly, the IOC urged the Chinese hosts of the 23rd Congress to associate all satellite meetings as far as possible with that Congress; members of satellite meetings, it was felt, should be registered members of the Congress.

## 19 The third century and Asia—the 23rd Congress, Beijing, 11 – 17 August 2002

Prior to the 1998 Congress, Permanent Secretary Bock visited Israel in the spring of 1996 to discuss the projected invitation from Israeli ornithologists; his host was Professor Yossi Leshem. His visit followed previous correspondence with Leshem; and at that time, the invitation from Israel was the only one in the offering. Bock was shown the projected Congress site in Jerusalem and met with a number of ornithologists who would be involved with the Congress. Because of the important migratory pathway over Israel well studied by Dr. Leshem, especially of large soaring birds, and because of Leshem's interest in working with students and ornithologists from neighboring countries, the theme of a congress in Jerusalem would be "Birds without boundaries." In the late fall of 1997, Bock also received an inquiry about a possible invitation from the People's Republic of China, with an invitation to visit Beijing in December 1997 to discuss this possibility with the large group of Beijing ornithologists who would be central to organizing and running the Congress. I did so and had extensive and detailed talks with those ornithologists who would be responsible for the Congress, as well as with Mr. Liu Feng who would serve as Assistant Secretary-General. I also had the opportunity to visit Professor Cheng Tso-Hsin, the guru of modern

Chinese ornithologists, but unfortunately in his hospital room. Professor Cheng gave me a greeting to the members of the 22nd Congress which was read at the opening of that Congress.

Immediately following the close of the Durban Congress, President Bock appointed Professor Xu Wei-Shu (China) as Secretary-General and Mr. Liu Feng (China) as Assistant Secretary-General of the 23rd Congress. Mr. Liu is a member of the Conference Section of the Chinese Academy of Sciences which is responsible for the running international meetings such as the ornithological congresses; Liu was the person designated for attending to all of the details for organizing and running the Beijing Congress. A National Committee was established under the chair of Professor Zheng Guang-Mei, with the necessary subcommittees to attend to all aspects of the Congress. President Bock visited Beijing for a third time early in January 2002 as the guest of Beijing Normal University to work with the central members of the Local Committee, and especially the remarkably efficient Mr. Liu, on many of details of organization, including the arrangement of sessions for the scientific program. The crested ibis *Nipponia nippon* was chosen appropriately as the symbol of the Congress in view of the free-living breeding colonies found of this endangered species in China and the very successful captive breeding program at the Changqing Nature Reserve. A set of postage stamps illustrating some Chinese birds was issued for the Congress, as was an excellent book, *Birds in China*, by Zheng Gaung-Mei and Zhang Cizu.

The SPC under the chair of Dr. Fernando Spina (Italy) was then appointed and set to work immediately. The committee met in June 2000, immediately following the meeting of the Society of Avian Evolution and Paleontology that was scheduled in Beijing in late May so that those members of the SPC interested in attending this meeting could do so. The SPC planned a program of 10 plenary lectures, 40 symposia, oral (limited to 200) and poster contributions and Round Table Discussions. In view of the problem with no-show poster papers at the 22nd Congress, the decision was made that submitted abstracts would be published in the program of the 23rd Congress only if the full congress registration was paid by 31 May 2002. Yet in spite of this arrangement, a number of persons withdrew at a late date, resulting in considerable work for Dr. Spina rearranging oral and poster sessions. A better system needs to be established for future congresses. The Chinese Local Committee decided to publish the plenary lectures as an issue of *Acta Zoologica Sinica* and the Congress Proceedings as a CR-ROM disk, and, if finances allowed, also as hard copy in the same journal.

Special emphasis was placed on the extraordinary Mesozoic fossil birds found in China, with one of the plenary lectures devoted to this topic. A request was also made to exhibit some of these fossil specimens at the Congress, which was done to the great advantage of the members. In addition, it was suggested that a special evening symposium in the form of a plenary *Presidential Debate* be held on the topic of the origin of birds, whether from early archosaurians or from later dinosaurs; President Bock was asked to invite the participants. The scientific program proved to be so full that overlaps between competing presentations could not be entirely avoided even by carefully planned concurrent sessions, a circumstance which in the end could not satisfy everyone. Although the debate on the origin of birds was held in the evening of the congress free day, when many members were tired from the field trips, it was still well attended, with many members expressing the view that it was one of the high points of the Congress.

The Beijing International Convention Center proved to be remarkably well set up for large congresses, with rooms of all sizes available for the different sessions. Movement between the different sessions was easy, within the same building; and a series of hotels with a range of prices were available nearby. Unfortunately, but not unexpectedly, the membership in the Congress was small, partly because the site was far from the main ornithological centers in Europe and North America and partly because fewer than anticipated ornithologists from eastern Asia were able to attend. Nevertheless there was much valuable interaction between Chinese ornithologists and those from the rest of the world, akin to that between Soviet and other ornithologists at the Moscow Congress in 1982.

The Welcoming Ceremony and Reception was held in the Convention Center on the evening of Sunday, 11 August, with greetings from Professor Zheng Gaung-Mei, Chair of the Chinese National Committee, Secretary-General Xu Wei-Shu, and several members of the academic community and government. But the highpoint came was a greeting from Mrs. Cheng, the widow of Professor Cheng Tso-Hsin who was truly the father of modern Chinese ornithology but who did not live to realize his dream of an international ornithological congress in China. Following the Closing Ceremony on the late afternoon of Saturday, 17 August, the final banquet was held in the Beijing Continental Grand Hotel in the evening. For the first time since the 4th Congress, the Presidential Address was not presented at the meeting because my vocal cords were still partly paralyzed as a result of an operation at the end of April, 2002 to repair an aneurysm in my descending thoracic aorta.

However, I was lucky to have recovered enough to be able to attend the Congress just four months after leaving the hospital, and to greet Congress members in the strangest of voices.

The major tour on the mid-congress free day of Thursday 15 August started with a pre-overnight stay at Songshan (northwest of Beijing) so that participants could get an early morning start to birding in the pine forest and then return to Beijing in time for the Presidential debate in the evening. A series of pre- and post-congress excursions were arranged to many different areas within China, including Tibet. For the group on the tour to the Changqing Nature Reserve, the high points were observing the roosting flight of herons and crested ibis *Nipponia nippon* in the evening after a day-long bus ride from Xi'an, followed by a visit to the captive breeding colony the next day, and seeing native dawn redwood trees (*Metasequoia glyptostroboides*, spotted by Richard Schodde) in the Qingling Mountains in Shaanxi Province far outside of their reported range.

The 23rd Congress hosted three satellite meetings that were announced in the Congress circular, namely the 2002 International Crane Workshop on 9–10 August, the International Pheasant Workshop on 15 August, and the 9th International Grouse Symposium on 18–24 August. Arrangements enmeshed very well with the program of the Congress, and satellite meetings should be encouraged for future congresses. With the termination of World Meetings by the restructured International Council of Bird Protection under BirdLife International, a regular international forum for presenting scientific studies concerning avian conservation has disappeared. The PEC discussed this matter, and recommended to the IOC that future congresses enlarge the program to include this field. This recommendation was accepted by the IOC which in turn directed the SPC for the 24th Congress to include topics of scientific study for bird protection in the scientific program of the Congress.

The meetings of the PEC and IOC were dominated by discussions of the future nature of the Congress and of the IOC, especially with respect to their financing. The *ad hoc* Financial Committee established by President Bock shortly after the 22nd Congress was unable to reach solutions, which was not surprising because such solutions are rarely clear and never simple. Another issue of concern was the role of the Vice-President. For good reasons, these are not specified in the Statutes except that his/her taking over the duties of the President if he/she is unable to carry on. It was recommended that the President assign specific tasks to the Vice-President, such as overseeing the activities of the Standing Committees, several of which had not operated over the past

four years. Also raised was the on-going lop-sidedness of the “membership classes” of the PEC, between experienced second-term renewals and novice first-term members, which had stemmed from the increase in numbers of elected members at the 20th Congress. These classes result from the arrangement whereby members can serve for two consequent terms, which most do. It had been assumed that the two “classes” would balance out rapidly to five old and five new due to turnovers, but this had not happened. Professor Fred Cooke, who could have served a second term, resigned to help restore the balance.

The slate of officers and elected members of the PEC was collated by Past-President P. Berthold for the nominating committee. Its recommendations included Professor Jacques Blondel (France) for President, Professor Dominique Homberger (United States) for Permanent Secretary, and Professor Jiro Kikkawa (Australia) for Honorary President, all of whom were recommended to the IOC and elected. Several excellent nominations were available for Vice-President and it was decided that the PEC would advance the names of Dr. Richard Schodde (Australia) and Professor John Wingfield (United States) to the IOC for their vote. At the second meeting of the IOC, Professor Wingfield was elected as Vice-President, together with the nominees for the other positions. The slate of new members of the IOC had been presented by Professor Cooke, chair of the nominating committee, to the PEC. After some discussion, including the recommendation that several persons be elected contingent on their attendance at the 2006 Congress, the slate was approved and forwarded to the IOC which accepted it at the same meeting.

Professor Franz Bairlein (Germany) presented to the PEC an invitation from German ornithologists to host the 24th Congress in Hamburg, which the PEC recommended in turn to the IOC; this invitation the IOC accepted with enthusiasm at its first meeting. Following the end of the 23rd Congress, President Blondel appointed Professor F. Bairlein as Secretary-General of the 24th Congress.

After the 23rd Congress in Asia, the only continent with resident ornithologists yet to stage an international ornithological congress is South America, the richest of all continents for birds. Efforts have been ongoing since the 18th Congress to elicit an invitation from a Neotropical country, but so far without success. During the meetings of both the PEC and the IOC at the 23rd Congress, considerable discussions were held on ways and actions to maximize the possibilities of holding a congress there in the near future, perhaps in 2010.

## 20 Closing

With the 23rd Congress, the International Ornithological Congresses entered its third century, developing from a small European colloquium with a primary focus on migratory pathways of birds into a major international conference covering a broad spectrum of avian biology. The increase in size and complexity can be readily appreciated if one compares the past five congresses with the first five congresses. Diverse aspects of the lives of birds have been covered in the last congresses that are far beyond the wildest imagination of ornithologists attending the 1st Congress. With a well-developed organizational system and a devoted group of international ornithologists, the future of these congresses appears strong. But there are several serious problems, some of which are the result of the success of the congresses themselves.

The first is that the congresses have grown large, with very full five working days. It is simply not possible for a person to experience everything that she/he would like to in that time; nor is it realistic to extend the length of the meetings much. If anything, many members are exhausted by the end of a congress, even given a free day at the middle of the week and a relaxing post-congress tour. A common complaint is that there is not sufficient time for one-to-one contact other congress goers. Many persons prefer smaller meetings on specialized topics, which certainly have the advantage of making it is easier to contact other members working in the field and to attend most if not all papers in the absence of concurrent sessions. Yet such meetings lack the depth, breadth and gravitas of full congresses.

Second is the problem of the increase in the number of additional international or major national meetings. Some of these are regional meetings, such as the Pan-African Congress, the Neotropical Ornithological Congress and the meetings of the more newly formed European Ornithologists' Union, which are necessary to permit regular interaction in areas where professional ornithologists are too few to hold viable meetings within their own country. It should be noted that the annual meetings of the American Ornithologists' Union serve this purpose for North America. Such regional meetings are especially valuable for educating and training younger workers. But a large number of specialist meetings have developed over the past several decades, such as the recently announced International Symposium on Ecology and Conservation of Steppe-Land Birds, many of which are restricted in scope. Most ornithologists have limited time and finances which constrain the number of international meetings that they can attend. All workers would be better served if such spe-

cialist meetings were attached, as satellites, to international ornithological congresses or appropriate major regional meetings. This certainly worked well at the 23rd Congress.

Third is the termination of the World Conferences of the International Council for Bird Protection with that organization's change to BirdLife International, resulting in a void for international discussion of scientific approaches to avian conservation. This need should be taken up by the international ornithological congresses because all aspects of bird protection and conservation have become a major component of ornithological endeavor throughout the world. Indeed most, if not all, ornithological activity in many countries is focused on conservation work, driven by the global decline in birdlife.

Fourth are the congress proceedings which have become increasingly large and expensive to publish. It must be noted that the Statutes state only that the Official Reports of congresses have to be published in some form. Moreover, there is the question about publishing new, exciting, ground-breaking material in congress proceedings. Most members feel, quite rightly in my view, that the proceedings are not the appropriate vehicle for publishing new ideas and findings, partly because of the long time required for collation and publication and partly because of the limited distribution of the proceedings. What the proceedings do so well, however, is to provide comprehensive overviews of the state of knowledge in the diverse fields of ornithology at the time, whether expressed in plenary lectures, symposia or even round table discussions. This is a role that has been advocated at the past several congresses. The expense of publication can be reduced considerably by using electronic methods to submit and edit manuscripts, and to publish the proceedings, as on CD-ROM disks, a method pioneered at the 22nd Congress in Durban. It allowed not only the publication of full plenary lectures but also full papers from symposia instead of longer abstracts which would have to be shortened even further because of publication costs. In the Durban Proceedings, an equivalent of 3 672 printed pages in *The Ostrich* format was published as a CD-ROM, far outstripping the size of any previous Congress Proceedings. Moreover, CD-ROM disks can be distributed to non-congress members at a reasonable price, thereby alleviating the problem of limited distribution. In present circumstances, if congress members wish to have a comprehensive and meaningful congress proceedings published, the use of CD-ROM disks may be the only way to achieve it.

Fifth is perhaps the most important issue of all: the growing problem of financing the IOC and especially the congresses. This has been a, if not the,

major topic of discussion for the PEC and the IOC at the 22nd and the 23rd Congresses. To date, the expenses incurred by the President and the Permanent Secretary have been generously absorbed by their own institutional or research funds; but there is no assurance that such support can continue indefinitely. In addition, new costs have arisen from maintaining an IOC home page on the WWW. For the congresses, it has always been necessary for Local Committees to raise funds to make up shortfalls in registration fees, and this can be particularly difficult in the first three years of operations, before registration fees begin to trickle in; the cost of the SPC meeting, in the middle of that period, is an especially large and critical drain. Although the Statutes of the IOC state that any funds left over from one congress should be passed to the next, this has never happened. In addition, funds are needed to support ornithologists with limited financial capacity to attend congresses. This is really an international responsibility, and should fall, not to the host country, but to the IOC itself. Unfortunately, almost no information is available on the finances of international ornithological congresses, as the financial operations for the congresses are run by local committees which are not required by the Statutes to publish them. Yet such information is needed before a sound financial plan can be established for the IOC.

In closing, I would like to add three personal notes. First, against the background of increasing specialization within biology, I am ever more strongly convinced of the importance of understanding the total biology of an entire group of organisms such as birds. Such analysis can be achieved only through the exchange of information among specialists in all areas of avian biology; and this exchange is best done in forums, such as the international ornithological congresses, which are devoted to all aspects of the biology of these organisms.

Secondly, my admiration is boundless for the groups of ornithologists who have organized and run the 23 international ornithological congresses we have had to date. In my duties as the Permanent Secretary of the IOC, I was always embarrassed when I urged different national groups of ornithologists to undertake the huge task of preparing the necessary invitation for a congress and then, if successful, having to plan and arrange it. The thanks of all ornithologists must go to these hard workers. I would like to single out several for special recognition: Rudolf Blasius (Brunswick) and Gustav von Hayek (Vienna) who were responsible for founding the first congress in 1884, Ernst Hartert (United Kingdom) who got the congress going once again in 1926 after World War II, and Donald Farner who established the modern form of the congress in 1978.

Thirdly, the preparation of this history was difficult because of a lack of information on many aspects of congress functions and events, due to skimpy Official Reports. I would plea for more detailed reports in the future and for members involved to deposit any congress-relevant papers, either in the IOC Archive at the Smithsonian Archives in Washington, D. C., or in some other well-established archive. At the same time, writing this history provided me with an excellent insight into international ornithology and the development of the congresses through all of their trials and tribulations from 1884 to 2002. Their great and consistent success is truly a tribute to the many, many ornithologists who have worked so hard for them. And now we can look forward to other groups who will continue this excellent tradition of the International Ornithological Congresses into the future.

Finally, I would like to thank most gratefully and sincerely the work of Dr. Richard Schodde who is serving as the general editor of the 23rd Congress Proceedings for his careful and thorough work in editing my manuscript.

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## Appendix

### List of Congresses and Proceedings

- 1) Vienna, 1884. President: Dr. Gustav F. R. Radde (German at Tbilisi, Georgia); Secretary-General: Professor Gustav von Hayek (Austria); Patron: H. R. H. Crown-Prince Rudolf of Austria-Hungary.  
1884–1886. Sitzungs-Protokolle des ersten internationalen Ornithologen-Congresses, der vom 7 bis 11 April in Wien abgehalten wurde. Verlag des Ornithologischen Vereines in Wien, 1884. Mittheilungen des Ornithologischen Vereins Wien, Band. vols. 8–10, numerous separate short articles.
- 2) Budapest, 1891. Presidents: Professor Victor Fatio (Switzerland) and Otto Herman (Hungary); Secretary-General: Dr. Geza von Horváth (Hungary).  
1891. [Bericht]... Zweiter internationaler Ornithologischer Congress. Edited by Geza von Horváth and Otto Herman, Budapest. Hungarian National Museum, Hungarian Committee of II International Ornithological Congress, Pt. 1 [Official Reports], 1–227 pp, Pt. 2 [Papers Presented], 1–238 pp, Pt 3 [Anatomie der Vögel by Fürbringer M] 1–48 pp.
- 3) Paris, 1900. President: Dr. Emile Oustalet (France); Secretary-General: G. Jean de Claybrooke (France); Honorary Presidents: Professor Alphonse Milne-Edwards (France, who passed away a four weeks prior to the Congress) and Baron Edmond de Selys-Longchamps (Belgium).  
1901. IIIe Congrès Ornithologique International Paris, 26–30 juin 1900. Compte rendu des séances publié par E. Oustalet... et J. de Claybrooke... Masson et Cie, Paris, xii + 503 pp. [= *Ornis*, vol. 11].
- 4) London, 1905. President: R. Bowdler Sharpe (United Kingdom); Secretary-General: Dr. Ernst. J. O. Hartert (United Kingdom) & J. Lewis Bonhote (United Kingdom); Patron: H. R. H. Prince of Wales George of the United Kingdom; Honorary Presidents: H. R. H. Prince Ferdinand of Bulgaria and Alfred Russell Wallace (United Kingdom).

1907. Proceedings of the IVth International Ornithological Congress, London, June 1905. Edited by Hartert EJO, Bonhote JL, Dulau & Co., London, 696 p. [= Ornith. vol. 14]
- 5) Berlin, 1910. President: Professor Anton Reichenow (Germany); Secretary-General: Herman Schalow (Germany); Schriftführer: Heinroth O (Germany), Kothe K (Germany); Honorary Presidents H. M. King Ferdinand of Bulgaria and H. R. M. Princess Dr. Therese of Bavaria.  
1911. Verhandlungen des Vth Internationaler Ornithologen-Kongresses. Berlin 30 Mai bis 4 Juni 1910. Herausgegeben von Herman Schalow. Deutsche Ornithologische Gesellschaft, Berlin, x + 1 186 pp.
- 6) Copenhagen, 1926. President: Dr. Ernst J. O. Hartert (United Kingdom); Secretary-General: E. Lehn Schiøler (Denmark); Honorary Presidents: H. R. H. Prince Knud of Denmark, Graft Murany of Coburg [former King of Bulgaria], Lord Walter Rothschild (United Kingdom).  
1929. Verhandlungen des VIth Internationalen Ornithologen-Kongresses in Kopenhagen, 1926. Edited by F. Steinbacher. Berlin, vi + 641 pp.
- 7) Amsterdam, 1930. President: Professor A. J. E. Lönnberg (Sweden); Secretary-General: Professor L. F. de Beaufort (The Netherlands).  
1931. Proceedings of the VIIth International Ornithological Congress at Amsterdam. Amsterdam, vii + 527 pp.
- 8) Oxford, 1934. President: Professor Erwin Stresemann (Germany); Secretary-General: Reverend Francis C. R. Jourdain (United Kingdom).  
1938. Proceedings of the VIIIth International Ornithological Congress, Oxford, July 1934. Edited by F. C. R. Jourdain. Oxford University Press, Oxford, x + 761 pp.
- 9) Rouen, 1938. President: Professor Alessandro Ghigi (Italy); Secretary-General: Jean Delacour (France).  
1938. IXe Congrès Ornithologique International Rouen, 9 au 13 Mai 1938. Edited by Jean Delacour. Rouen, 543 pp.
- 10) Uppsala, 1950. President: Dr. Alexander Wetmore (United States); Secretary-General: Professor Sven Hörstadius (Sweden).  
1951. Proceedings of the Xth International Ornithological Congress, Uppsala, June 1950. Edited by Sven Hörstadius. Almqvist & Wiksells, Uppsala, 662 pp.
- 11) Basel, 1954. President: Sir Landsborough Thomson (United Kingdom); Secretary-General: Professor Adolf Portmann (Switzerland).  
1955. Acta XI Congressus Internationalis Ornithologici. Basel, 29. V – 5. VI. 1954. Herausgegeben von Adolf Portmann und Ernst Sutter. Birkhäuser Verlag, Basel und Stuttgart, 680 pp.
- 12) Helsinki, 1958. President: Professor Jacques Berlioz (France); Secretary-General: Professor Lars von Haartman (Finland).  
1960. Proceedings of the XIIth International Ornithological Congress, Helsinki, 4 – 12. VI. 1958. Edited by G. Bergmann, KO. Donner & L. v. Haartman. Tilgmannin Kirjapaino, Helsinki, 2 vols, 820 pp.
- 13) Ithaca, 1962. President: Professor Ernst Mayr (United States); Secretary-General: Professor Charles G. Sibley (United States).  
1963. Proceedings of the XIIIth International Ornithological Congress, Ithaca, 17 – 24 June 1962. Edited by CG Sibley, JJ Hickey, & MB Hickey. American Ornithologists' Union, Lawrence, Kansas, 2 vols, XVI + 1 246 pp.
- 14) Oxford, 1966. President: Dr. David Lack (United Kingdom); Secretary-General: Dr. Niko Tinbergen (United Kingdom).  
1967. Proceedings of the XIVth International Ornithological Congress, Oxford, 24 – 30 July 1966. Edited by DW Snow. Blackwell Scientific Publications, Oxford and Edinburgh, xxiv + 405 pp.
- 15) Den Haag, 1970. President: Dr. Niko Tinbergen 1966 – 1969 (United Kingdom), Professor Finn Salomonsen 1969 – 1970 (Denmark); Secretary-General: Professor Karel Voous (The Netherlands); Patron: H. R. H. Prince Bernhard of The Netherlands.
1972. Proceedings of the XVth International Ornithological Congress. The Hague, 30 August – 5 September 1970. Edited by KH Voous. E. J. Brill, Leiden, VIII + 745 pp.
- 16) Canberra, 1974. President: Professor Jean Dorst (France); Secretary-General: Dr. Harry J. Frith (Australia); Patron: H. R. H. Prince Philip, Duke of Edinburgh.  
1976. Proceedings of the XVIth International Ornithological Congress, Canberra, 12 – 17 August 1974. Edited by HJ Frith and JH Calaby. Australian Academy of Science, Canberra, XVIII + 765 pp.
- 17) Berlin, 1978. President: Professor Donald S. Farner (United States); Secretary-General: Dr. Rolf Nöhring (Germany).  
1980. Acta XVIIth Congressus Internationalis Ornithologici, Berlin, 5 – 11 VI. 1978. Herausgegeben von Rolf Nöhring. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin, 2 vols, 1 335 pp.
- 18) Moscow, 1982. President: Professor Lars von Haartman (Finland); Secretary-General: Professor Valery D. Ilyichev (Russia, USSR).  
1985. Acta XVIIIth Congressus Internationalis Ornithologici, Moscow, August 16 – 24, 1982. Edited by VD Ilyichev and VM Gavrilov. "Nauka", Moscow, 2 vols, 1 335 pp.
- 19) Ottawa, 1986. President: Professor Klaus Immelmann (Germany); Secretary-General: Dr. Henri Ouellet (Canada).  
1988. Acta XIXth Congressus Internationalis Ornithologici, Ottawa, 22 – 29. VI. 1986. Edited by H. Ouellet. University of Ottawa Press, Ottawa, 2 vols, 2 815 pp.
- 20) Christchurch, 1990. President: Professor Charles G. Sibley (United States); Vice-President Professor Jan K. Pinowski (Poland); Secretary-General: Dr. Ben Bell (New Zealand); Permanent Secretary: Professor Walter J. Bock (United States); Patron: H. R. H. Prince Philip, Duke of Edinburgh; Honorary President: Dr. N. K. Kuroda (Japan); Honorary Vice-Presidents: Professor Helmut Sick (Brazil), Professor Hsu Wei-shu (China).  
1991. Acta XXth Congressus Internationalis Ornithologici, Christchurch, 2 – 9 December 1990. Edited by Ben Bell et al. New Zealand Ornithological Congress Trust Board, 4 vols, 2 568 pp.
- 21) Vienna, 1994. President: Professor Christopher M. Perrins (United Kingdom); Vice-President: Professor Svein Haftorn (Sweden); Secretary-General: Professor John Dittami (Austria); Permanent Secretary: Professor Walter J. Bock (United States); Honorary President: Professor Karel Voous (The Netherlands).  
1996. Acta XXIth Congressus Internationalis Ornithologici, Vienna, 20 – 25 August 1994. Edited by J Wingfield & J Coulson. British Ornithologists' Union, 1 – 128 + A129 – A146 (Ibis, Vol. 138, No. 1, 128 pp.).
- 22) Durban, 1998. President: Professor Peter Berthold (Germany); Vice-President: Dr. Janet Kear (United Kingdom); Secretary-General: Dr. Aldo Berruti (South Africa); Permanent Secretary: Professor Walter J. Bock (United States); Honorary President: Professor Chang Tso-Hsin (China).  
1999. Plenary Papers. 22nd International Ornithological Congress, Durban 16 – 22 August 1998. Edited by NJ Adams & RH Slotow, Ostrich, 70: 1 – 103.  
1999. Proceedings of the 22nd International Ornithological Congress, 16 – 22 August 1998, Durban. Edited by N Adams & R Slotow. Birdlife South Africa, Johannesburg, CD-ROM disk.
- 23) Beijing, 2002. President: Professor Walter J. Bock (United States); Vice-President: Professor Jacques Blondel (France); Secretary-General: Professor Xu Wei-Shu (China); Assistant Secretary-General: Mr. Liu Feng (China); Permanent Secretary: Professor Dominique G. Homberger (United States); Honorary President: Professor Ernst Sutter (Switzerland).
- 24) Hamburg, 2006. President: Professor Jacques Blondel (France); Vice-President: Professor John C. Wingfield (United States); Secretary-General: Professor Franz Bairlein (Germany); Permanent Secretary: Professor Dominique G. Homberger (United States); Honorary President: Professor Jiro Kikkawa (Australia).



## Mesozoic birds of China: an introduction and review<sup>\*</sup>

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**Abstract** Over the last decade, more Mesozoic birds have been discovered from the Early Cretaceous of Liaoning Province in northeast China than from any other region on earth. Chinese Mesozoic birds represent the earliest significant avian diversification yet known after the oldest known bird *Archaeopteryx* appeared in the fossil record about 20 million years earlier. They not only include a long-tailed form reminiscent of dinosaurian ancestry but also comprise many other special or derived forms, such as the oldest-known beaked bird, the largest Early Cretaceous bird, the most primitive enantiornithine bird and the best preserved ornithurine bird, with a flight apparatus nearly identical to that of modern birds. Remarkable evolutionary, morphological and ecological differentiation, such as in flight, size and diet, are well documented by the Chinese fossils. The long-tailed, basal bird *Jeholornis* bears a remarkable resemblance to dromaeosaur dinosaurs, thus providing important clues in support of the dinosaurian origin of birds. Chinese Early Cretaceous birds, as well as arboreal dinosaurs of the same age in China, also provide compelling evidence for the arboreal hypothesis of the origin of avian flight. The ‘Dinosaur-trees-down’ hypothesis, which combines the dinosaurian origin of birds and the arboreal hypothesis of avian flight, is thus well collaborated. Because feathers were present in various dinosaurs, the association of endothermy with feathers becomes purely speculative; endothermy probably did not develop in birds until the Early Cretaceous [*Acta Zoologica Sinica* 50 (6): 913–920, 2004].

**Key words** Mesozoic, Fossil, Bird, Origin, China

## 中国中生代的鸟类：介绍及综述<sup>\*</sup>

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**摘要** 最近十来年, 中国辽宁发现的早白垩世的鸟类化石超过了世界上其它任何一个地区。中国的中生代鸟类化石代表了始祖鸟化石之后鸟类历史上第一次显著的分异。它们不仅包括了带有明显恐龙祖先特征的长尾的鸟类, 而且还包括了许多进步或特化的种类, 如早白垩世最大的鸟类, 最原始的反鸟类, 以及保存最好的、飞行结构和现生鸟类几乎一样的今鸟类。这些早期鸟类在诸如飞行、大小和食性等所反映的演化、形态和生态学特征等方面出现了重大的分异。具有长尾骨骼的原始基于鸟类热河鸟和驰龙类具有的相似性, 进一步支持了鸟类起源于恐龙的学说。中国发现的早白垩世的鸟类以及树栖的恐龙化石还为鸟类飞行的树栖起源假说提供了十分重要的证据。“恐龙下树”的假说结合了鸟类起源于恐龙的学说和鸟类飞行的树栖起源学说, 因此也得到了化石证据的支持。由于多种恐龙带有羽毛, 因此羽毛不一定代表了恒温。恒温的鸟类可能到了早白垩世的进步鸟类中才开始出现 [*动物学报* 50 (6): 913–920, 2004]。

**关键词** 中生代 化石 鸟类 起源 中国

### 1 Introduction: historical and geological background

*Archaeopteryx* has long been held as the oldest and most primitive bird ever since its discovery in late Jurassic sediments in 1861 (Wellnhofer, 1992); yet since then the fossil history of birds has only become

relatively well documented from the Late Cretaceous on (Martin, 1991). Little, accordingly, has been known about birds in the intervening period until the last two decades of the 20th century when Early Cretaceous avian fossils began to be discovered in Mongolia (Kurochkin, 1985), Spain (Sanz et al., 1995, 1996) and China (Zhou, 2002; Zhou and Zhang,

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2002a, b). Since then, the discoveries of Early Cretaceous birds in western Liaoning Province in north-east China have not only improved our understanding of the early evolution of birds significantly but also made China the most important area for the study of early birds today.

Although the results of finding Mesozoic birds in China did not explode upon the world until the early 1990s, the discovery of the fossil sites dates back to 1982. Three stages of discovery can be recognized. From 1982 to 1993, fossils were found in the Jiufotang Formation, mainly in Gansu Province in northwest China (Hou and Liu, 1984), in Inner Mongolia in northern China (Hou, 1994) and at Chaoyang County in western Liaoning Province, northeast China (Serenio and Rao, 1992; Zhou et al., 1992; Hou and Zhang, 1993; Zhou, 1995; Martin and Zhou, 1997). The fossils include mainly enantiornithines (e.g., *Sinornis*, *Cathayornis* and *Otogornis*) and a few incomplete ornithurines (*Gansus*, *Chaoyangia* and *Songlingornis*).

Then, from 1994 to 1999, hundreds of fossils were found in the Yixian Formation, which underlies the Jiufotang Formation, at Beipiao (Hou et al., 1995, 1996, 1999a, b; Zhou and Hou, 1998; Chiappe et al., 1999) and Lingyuan (Hou and Chen, 1999) in western Liaoning Province, as well as in neighboring northern Hebei Province (Zhang and Zhou, 2000). The fossils include the abundant *Confuciusornis*, a few primitive enantiornithines (*Protopteryx*, *Eoenantiornis* and *Liaoxiornis*), and one primitive ornithurine *Liaoningornis*. Since 2000, many more new taxa of birds have been described from the Jiufotang Formation following discoveries at several new localities near Chaoyang City and in Yixian County of Jinzhou City in Liaoning Province (Zhang and Zhou, 2001; Zhou and Zhang, 2001b, 2002a, b). The fossils include some completely articulated ornithurine birds (*Yixianornis* and *Yanornis*), the largest Early Cretaceous bird *Sapeornis*, and the long-tailed *Jeholornis* and enantiornithines *Longipteryx* as well as *Confuciusornis*.

Without exception, all Mesozoic birds in China have been found in lacustrine Cretaceous sediments, primarily the Yixian Formation and the overlying Jiufotang Formation. Both  $^{40}\text{Ar}/^{39}\text{Ar}$  and U-Pb zircon dating of the Yixian Formation suggests an age of about 125 million years before present (Swisher et al., 1999, 2002; Wang et al., 2001), with the Jiufotang Formation slightly younger, around 120 million years before present (Eberth et al., 1993; He et al., 2004).

The exceptional abundance and diversity of early avian populations in western Liaoning can probably be attributed to frequent volcanic activity and the devel-

opment of many partly isolated inter-mountain lakes during the Early Cretaceous (Chen, 1988). Mass mortality caused by volcanic eruptions resulted in the preservation of not only hundreds of individuals of *Confuciusornis* but also many juvenile individuals of early birds. Feathers were preserved either attached to complete skeletons or separated. In some unusual cases, nearly complete plumage was preserved without any skeletal elements.

All known Mesozoic bird fossils in China belong to the Jehol Biota, which is endemic to East Asia. Although this biota includes some relics that survived from the Late Jurassic or earlier, it mostly comprises taxa typical of Early Cretaceous times and indicates that East Asia was then a center of diversification for various dinosaurian lineages. Abundant vertebrates, invertebrates and plant fossils are equally well-preserved and -known. Probably the most significant among them are the many feathered dinosaurs, *Sinosauropteryx*, *Protarchaeopteryx*, *Caudipteryx*, *Beipiaosaurus*, *Sinornithosaurus* and *Microraptor* (Chen et al., 1998; Ji et al., 1998; Xu et al., 1999a, b, 2000, 2003; Zhou and Wang, 2000; Zhou et al., 2000), the early mammals *Zhangheotherium*, *Jeholodens*, *Eomaia*, *Repenomamus*, *Sinobaatar*, *Sinodelphys* (Hu et al., 1997; Ji et al., 1999, 2002; Wang et al., 2001; Hu and Wang, 2002; Luo et al., 2003), and putative angiosperms such as *Archaeofructus* (Sun et al., 1998, 2002) and the non-controversial angiosperm *Sinocarpus* (Leng and Friis, 2003). Other important vertebrate groups include fishes (acipenseriforms, bowfins and teleosts), amphibians (frogs and salamanders) (Wang et al., 2001; Gao and Shubin, 2001), turtles *Manchurochelys* (Li and Liu, 1999), aquatic reptiles (e.g., *Monjurosuchus* and *Hapalosaurus*) (Gao et al., 2000), lizards (*Yabeinosaurus*), pterosaurs (pterodactyls and anurognathids) (Wang et al., 2002), as well as other dinosaurs that did not have feathers (psittacosaurids, iguanodontids, oviraptorids, troodontids, ankylosaurids and sauropods) (Wang and Xu, 2001; Xu et al., 2001, 2002a, b). The invertebrates include insects, spiders, crustaceans (Ostracoda, Notostraca, Conchostraca, Decapoda, Peracarida), and bivalves and gastropods. The flora is dominated by conifers but also contains bryophytes, lycopods, sphenopsids, ferns, Bennettiales, Czekanowskiales, Ginkgoales, Gnetales and putative angiosperms (Zhang et al., 2001). It is notable that among the over one thousand species of insects, many are nectar-feeders with long tubular mouth-parts (Ren, 1998).

## 2 Implications for the early evolution and diversification of birds

The Mesozoic avian fossils of China represent some of the most basal birds known in avian evolution, notably *Jeholornis*, *Sapeornis* and *Confuciusornis* (Fig. 1). These birds form the sister groups of nearly all major groups of extinct and extant birds, including Enantiornithes and Ornithurae (Martin, 1991). Among them, *Jeholornis* is most similar to *Archaeopteryx* in terms of primitiveness. It retained an unreduced skeletal tail and was toothed, though the teeth were reduced and its flight structures are obviously much improved (Zhou and Zhang, 2002b). *Sapeornis* has a tail reduced to a pygostyle, yet it still retained a short and robust coracoid nearly identical to that of *Archaeopteryx*; interestingly, it is the largest bird known from the Early Cretaceous and it is also larger than *Archaeopteryx* (Zhou and Zhang, 2002a). Its extremely elongated forelimbs suggest that it may have been able to soar in flight. *Confuciusornis* represents the oldest known bird with a horny beak. Like *Sapeornis*, *Confuciusornis* has a pygostyle, but its strut-like coracoid indicates more powerful capability in flight. Sets of long (male) and short (female) tail feathers also suggest sexual dimorphism; and the unusual accumulation of massed individuals at a site indicates that *Confuciusornis* gathered socially in flocks.

The majority of early Chinese birds belong to the prevalent Mesozoic avian group, Enantiornithes, which became extinct by the end of that era. These birds were all toothed, arboreal, and usually small, and, with a well-fused carpometacarpus and reduced manual digits, were evidently capable of powerful flapping flight (Zhou, 2002). On the other hand, they lack a deep keel on the sternum and their coracoids lack a well-developed procoracoid; therefore the triosseal canal characteristic of modern birds was probably missing. Among them, *Protopteryx* is the most primitive, with unique tail feathers showing features transitional between scales and modern feathers (Zhang and Zhou, 2000); yet it also possessed the advanced flight structure, the alula, which is absent in *Archaeopteryx* and *Confuciusornis*. *Eoenantiornis* also had the alula (Hou et al., 1999b). Another enantiornithine *Longipteryx* is specialized with relatively long wings and short hindlimbs indicative of a perch-and-pounce life style similar to that of a kingfisher, i. e. perching in trees near water and catching fish from soaring sweeps over the surface of lakes (Zhang and Zhou, 2001).

Another major group of birds in the Early Cretaceous deposits of China is the Ornithurae, to which all extant birds belong, as well as their extinct kin

that first appeared then. All Chinese fossil ornithurines were toothed, like other Mesozoic birds. Among them, *Liaoningornis* from the Yixian Formation is the smallest and most primitive; it is also obviously arboreal (Hou et al., 1996). Other forms such as *Yixianornis* and *Yanornis* are from the Jiufotang Formation and are similar to *Confuciusornis* in size, much larger than contemporaneous enantiornithines (Zhou and Zhang, 2001b). Unlike *Confuciusornis* and enantiornithines, which are mainly perching forms, the ornithurines lived mostly near the water, perhaps as waders, as indicated by long pedal toes and toe proportions. They probably fed on fish and other aquatic animals. Although they possessed flight structures barely distinguishable from those of modern birds (well-fused carpometacarpus, well-developed procoracoid, and deep keel on the sternum), they also retained some primitive traits such as teeth, a pubic symphysis, gastralia and wing claws as in *Archaeopteryx*, *Jeholornis*, *Sapeornis* and the enantiornithines. Thus, they could not have been the immediate ancestors of modern birds. From known evidence, modern orders of birds did not arise until at least the Mid Cretaceous, no earlier than 110 million years before present.

The Early Cretaceous birds of China provide the best material yet for studying the early evolution of birds, between Late Jurassic (*Archaeopteryx*) and Late Cretaceous times. The Chinese deposits reveal and record in detail, for the first time, a remarkable diversification of birds in the Early Cretaceous. While many primitive basal forms continued to survive then, a group of birds of modern appearance, the ornithurines, began to evolve in a direction that finally led to modern birds. Early Cretaceous birds show not only remarkable evolutionary, morphological and ecological differentiation, but also significant variation in size. Moreover, although relatively little is known about the feeding habits of these birds, differentiation in dietary habits had obviously developed. Thus stomachs of the long-tailed *Jeholornis* preserved seeds, convincing evidence of granivory, while those of some ornithurine birds such as *Yanornis* preserved fish, consistent with the life style reconstructed above.

## 3 Implications for the origin of birds

Since its discovery, *Archaeopteryx* has been regarded as one of the foremost links between birds and reptiles. Further, as the oldest bird, it has also become the focal source for perceptions of the ancestral bird. Since the 1970s, John Ostrom has rejuvenated the dinosaurian hypothesis of the origin of birds based on a detailed comparison of *Archaeopteryx* with theropod dinosaurs (Ostrom, 1976).

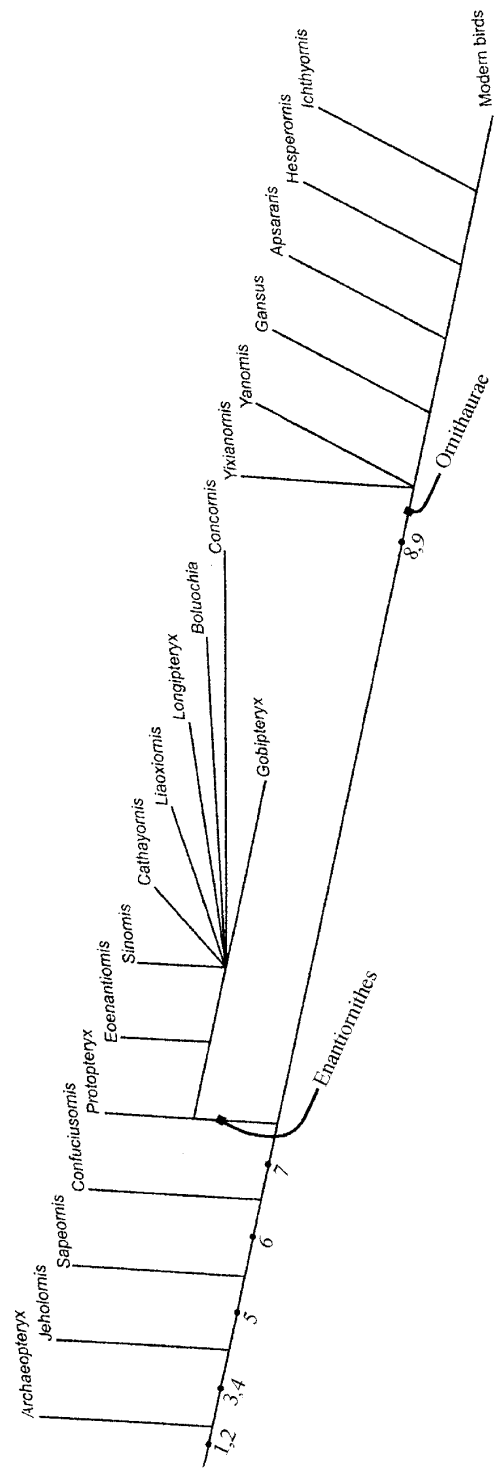


Fig.1 Cladogram showing the phylogenetic relationship of the major Mesozoic birds of China

Numerals 1–9 represent the appearance of important morphological features in the early evolution of birds. 1: Asymmetry of flight feathers. 2: Reversed hallux. 3: Carpometacarpus. 4: Lateral trabeculae of the sternum. 5: Pygostyle. 6: Horny beak. 7: Alula. 8: Elongated and well-keeled sternum. 9: Well-developed procoracoid and triosseal canal.

*Jeholornis* from the late Early Cretaceous of China (Zhou and Zhang, 2002b) is now the second bird

known with a complete long skeletal tail. Perhaps more importantly, its caudal vertebrae, like those in *Archaeopteryx*, have long elongated chevrons and prezagopophyses similar to those of dromaeosaurid dinosaurs, further evidence linking birds with this particular group of theropods. Another similarity shared with some theropods is a relatively large sickle-shaped claw on the second pedal digit. Fan-shaped tail feathers in *Jeholornis* also bear a remarkable resemblance to those of theropods such as *Caudipteryx* and the dromaeosaurids.

It may be significant that nearly all of the known theropods thought to be closely related to birds (specifically, the maniraptorans) have been collected from deposits younger than the age of the oldest bird, *Archaeopteryx*. Phylogenetically, this does not negate the dinosaurian origin hypothesis of birds. Rather, for critics of this hypothesis, it poses a problem: could the bird-like dinosaurs have developed their many bird-like traits secondarily, or, in other words, are the similarities shared with birds the result of parallel evolution?

It is equally noteworthy that up to ten years ago, before the discoveries of feathered dinosaurs from the Liaoning Province in China, the most bird-like dinosaurs (= the closest relatives of birds) that were used for phylogenetic comparisons with birds came from the Late Cretaceous, such as *Deinonychus*, *Dromaeosaurus* and *Velociraptor*. The Chinese fossils have now pushed back their record to the Early Cretaceous. Yet Early Cretaceous times post-date the oldest known bird by about 20 million years, and are still too young for the origin of birds. Significantly, the recently described maniraptoran *Epidendrosaurus*, which was believed to be very close to the transition between dinosaurs and birds, comes from an older deposit bordering western Liaoning: the Daohugou Formation in Inner Mongolia (Zhang et al., 2002). The age of the Daohugou Formation is still controversial, ranging from Middle Jurassic to Early Cretaceous according to different workers. If this is confirmed, then it fills another big temporal gap that has perplexed paleontologists about the origin of birds.

Although *Jeholornis* is obviously a more advanced bird than *Archaeopteryx*, its tail comprises more caudal vertebrae and more elongated skeletal chevrons, which in turn appear more like those of the dromaeosaurids. This suggests that *Archaeopteryx* may be no more than a side branch on the avian evolutionary tree. On the other hand, it can also be argued that the longer and more dinosaur-like tail of *Jeholornis* is a secondary adaptation. In other words, if the feathered dinosaurs such as dromaeosaurids are secondarily flightless, *Jeholornis* might be viewed as

a transition between *Archaeopteryx* and the secondarily flightless Cretaceous birds (Martin, pers. comm.). Despite this inspiring and tantalizing thought, we have to admit that a complete and compelling phylogenetic analysis has still to be presented for the view that feathered dromaeosaurids and oviraptorids are indeed more derived than the most primitive birds such as *Archaeopteryx* and *Jeholornis*. In the interim, we continue to regard *Jeholornis* as a bird that retained some very primitive traits from dinosaurian ancestors.

#### 4 Implications for the origin of flight in birds

Controversy over the origin of the flight has never been as heated as it has over the origin of birds themselves; yet the two are tightly connected. The competing 'Ground-up' and 'Trees-down' hypotheses for the origin of avian flight are often linked automatically with dinosaurian and non-dinosaurian origins respectively (Ostrom, 1986; Feduccia, 1999). Yet recently, a third and growing view accepts the dinosaurian origin of birds together with the arboreal hypothesis for the origin of flight. This we coin as the 'Dinosaur-trees-down' hypothesis. The 'Dinosaur-trees-down' hypothesis encapsulates our view because we believe that (1) a majority of evidence supports the dinosaurian origin of birds, and (2) as we show below, all current fossil evidence from both early birds and dinosaurs supports the arboreal hypothesis for the origin of flight.

We believe that the habit and life style of the most primitive birds and their closest ancestors is central to the issue of the origin of the flight. The recent record of arboreal dinosaurs from the Early Cretaceous of Liaoning provides the best evidence yet for testing our hypothesis. But how can we reconstruct the habits of extinct forms? The curvature of the pedal claws has been shown to be a simple but effective means of distinguishing between ground-living and tree-living birds (Feduccia, 1993). The shape of the cross-section of the claws can also be useful here (Yalden, 1997), and also the proportions of pedal digits, i. e., distal toes are relatively longer in arboreal forms and *vice versa* (Hopson, 2001; Zhou and Farlow, 2001).

*Microraptor* is a small dromaeosaurid dinosaur with foot features that indicate an arboreal habit (Xu et al., 2000). Such traits include slender and recurved pedal claws, a distally positioned digit I, and elongated penultimate phalanges, all comparable to those of arboreal birds (Xu et al., 2000). Probably just as significantly, *Sinornithosaurus*, another dromaeosaurid from the Early Cretaceous of China, has feet covered by elongated feathers, strongly suggest-

ing that it was also arboreal. *Epidendrosaurus* from the Late Mesozoic of Inner Mongolia, the oldest known maniraptoran and occupying a position very close to the transition from dinosaurs to birds, seems to have been arboreal too (Zhang et al., 2002). Evidence for this is to be found not only in toe proportions (the penultimate phalanges are longer than the phalanges immediately proximal to them), but also in the surprisingly distal position of the first pedal digit. The first pedal digit is relatively long and is positioned so far distally that the distal ends of the four metatarsal bones are nearly on the same level; it is a construction very similar to that in advanced arboreal birds.

The most primitive bird *Archaeopteryx* has the pedal claw curved like that of a trunk-climbing bird (Feduccia, 1993). *Confuciusornis* is similar, not just in the curvature of the claws but also in cross-section shape (Zhou and Farlow, 2001), indicating that both birds possessed climbing capability. The toe proportions of *Archaeopteryx* and *Confuciusornis* indicate that both could perch; yet that capability is still not as good as in typical perching birds (Zhou and Farlow, 2001). Pedal toe proportions in *Jeholornis* are similar to those in most other basal birds, and are more-or-less transitional between those of a dinosaurian ancestor and more advanced perching birds such as *Sinornis* (Serenio and Rao, 1992) and *Boluochia* (Zhou, 1995).

It should be pointed out that the foot is not the only apparatus involved in climbing and the arboreal life of early birds and feathered maniraptoran dinosaurs. The manual toe proportions of these animals are similar to those in the foot of arboreal birds, with elongated penultimate phalanges. We interpret such structures as adaptations for grasping tree branches. As the perching capability of the foot improved, so the climbing or grasping role of the forelimb declined (claws reduced, loss of phalanges and shortening of distal phalanges). Such trends are well documented in the fossil forms from the Early Cretaceous of China.

Evidently then, all the most basal birds were arboreal; and their closest dinosaurian relatives were arboreal too. From all this evidence, we find the arboreal hypothesis the most likely explanation for the origin of flight in birds. Further, one of the major differences between birds and dinosaurs is the reversed hallux in birds, which we interpret as an adaptation for improved arboreal life, again consistent with the arboreal hypothesis scenario.

During the evolution of birds and flapping flight, feathers evolved in their own way. The initial unbranched feathers in basal coelurosaurs were probably only for display or thermoregulation; but in arboreal

maniraptoran dinosaurs, primitive feathers were probably used to help in balance and/or steering while climbing or jumping, or helped to reduce the rate of descent while falling or jumping to the ground. But only birds evolved asymmetric flight feathers for flapping flight; and from there more derived feathered structures, such as the alula, developed in later, more advanced birds such as the enantiornithines.

So the 'Ground-up' hypothesis for the origin of flight of birds is not supported by any substantial fossil evidence; on the contrary, the 'Dinosaur-trees-down' hypothesis is not only consistent with the phylogenetic background for the origin of birds, but also with all reconstructions of the arboreal habit of early birds, as well as their putative ancestors.

## 5 Feathers and endothermy

The issue of the origin of feathers has been dealt with by us in a separate paper in the Proceedings of this Congress, so here we will only focus on one topic, the relationship between feathers and endothermy. All modern birds are hot-blooded; but what about fossil birds? Feathers have been considered a unique characteristic of endothermic birds. The discovery of feathered dinosaurs, however, has not only changed our view on the origin of birds and the life of dinosaurs, but also of the role of feathers in avian evolution. The basal coelurosaurid *Sinosauropteryx* has proto-feathers, but their function remains speculative; they could have functioned either for thermoregulation or display. As this dinosaur was a bipedal cursorial animal, its protofeathers were not yet linked with flight. It is also notable that the crest in feathered dinosaurs, including *Sinosauropteryx* and dromaeosaurids, seems to provide evidence for the display hypothesis for the origin of feathers.

It is generally accepted that dinosaurs are more similar to birds than extant reptiles in terms of growth rates (Zhang et al., 1999; Erickson et al., 2001; Padian et al., 2001), an assessment consistent with the currently popular view that birds are the crow group of the Dinosauria. But how, exactly, are dinosaurs close to extant birds in physiology? Are they still ectotherms or not? Erickson et al. (2001) found that all dinosaurs grew at rates more rapid than those of extant reptiles; but as a whole the rates were not intermediate between, nor equivalent to, those in birds and mammals. Erickson et al. (2001) also noticed that non-avian dinosaurs never attained the extremely rapid rates found in extant altricial birds; even the largest sauropods would have grown at rates half those of a scaled-up altricial bird. Small dinosaurs, moreover, tended to have slow growth rates. Erickson et al. (2001) estimated that small non-avian dinosaurs have growth rates typically 2–7

times slower than those of precocial birds of similar size.

It is notable that the recently discovered Chinese dromaeosaurids (e.g. *Microraptor*), which are close relatives of birds, are very small; they probably had much slower growth rates than large dinosaurs. The adaptation towards small size during the transition from dinosaurs to birds does not seem to be advantageous for the evolution of endothermy. As Padian et al. (2001) have correctly pointed out, reduction in body size was almost certainly associated with a reduction in the time needed to reach adult size. The relative elongation of forelimbs and feathers, coincident with a phyletic reduction in adult size, would have been advantageous for the inception of flight by decreasing wing loading and improving the power-to-weight ratio. Reduction in size continued on into the early evolution of birds. All early enantiornithines are smaller than such basal forms as *Archaeopteryx*, *Sapeornis* and *Jeholornis*.

There is currently no compelling evidence that any dinosaurs were hot-blooded. The association of feathers with endothermy is purely speculative, not only for dinosaurs but probably also for some early birds. Bone histology studies show that enantiornithines lacked vascular canals and had clear lines of arrested growth (LAGs), which are distinct from those of *Confuciusornis* and modern birds. These features are commonly found in extant ectothermic reptiles such as crocodiles. Basal birds probably did not possess the physiological organization of modern birds, and they could have been ectothermic. The late Cretaceous ornithurine birds *Hesperornis* and *Ichthyornis* have higher vascularity and lack LAGs, showing greater similarity to extant birds. Based on these data, Padian et al. (2001) suggested that modern birds gained a fully endothermic metabolism gradually. Zhang et al. (1999) compared the bone histology of *Confuciusornis* with that of an extant crocodile *Alligator* and modern birds. They concluded that *Confuciusornis* was more like extant birds than enantiornithines, and further suggested that it could be endothermic. Because *Confuciusornis* is phylogenetically more basal than the enantiornithines, its endothermy probably evolved independently.

Early Cretaceous ornithurine birds such as *Yixianornis* and *Yanornis* from China possess flight structures almost indistinguishable from those of modern birds (Zhou and Zhang, 2001b). Phylogenetically they are also much closer to extant birds than the enantiornithines and other basal forms such as *Confuciusornis*. Even though they retained some primitive traits that preclude them from being the direct ancestor of modern birds, the early ornithurines represented the highest evolutionary level attained by

birds in the Early Cretaceous. In contrast to the enantiornithines, which were generally small in the Early Cretaceous, the ornithurines were all of considerable size, indicating that they had faster growth rates. It is this group that probably first possessed true endothermy among early birds.

Although some of the features thought to be unique to birds, such as feathers, are now known to have appeared earlier in dinosaurian ancestors, there are still many fundamental traits in modern birds that did not arise until later stages in avian evolution. Thus the horny beak is first known to have appeared in the Early Cretaceous *Confuciusornis*, a pygostyle first appeared in such basal birds as *Sapeornis*, an alula first appeared in the Early Cretaceous *Protopteryx*, and well-developed procoracoids, triosseal canals and sternal keels first appeared in the Early Cretaceous ornithurines. The Early Cretaceous is undoubtedly a critical stage for the evolution of birds, and we believe that like many other features, avian endothermy first appeared then.

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## Bird flight

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**Abstract** The current states of knowledge concerning flight mechanics, kinematics and morphological adaptations for flight are reviewed. The basis for force generation, including airfoil action and vorticity, and the power required for flight, are discussed first, followed by the kinematics of flapping flight and gait changes, and scaling issues for flight. The importance of the shape of wing and tail for flight performance is elucidated, concluding with an analysis of the flight capability of *Archaeopteryx* [Acta Zoologica Sinica 50 (6): 921–935, 2004].

**Key words** Flight, Aerodynamics, *Archaeopteryx*, Kinematics, Vortices, Wing characteristics

## 鸟类的飞翔

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**摘要** 本文综述了目前对鸟类飞翔的研究, 包括飞翔机制、运动学和形态适应等问题。首先讨论动力产生的基础包括翼型运动和气体旋涡以及飞翔需要的动力, 而后论述振翅飞翔和姿势变换的运动学原理及量化飞翔强度, 阐明了翼部和尾部外形对飞翔的重要作用, 并分析了始祖鸟的飞翔能力 [动物学报 50 (6): 921–935, 2004]。

**关键词** 飞翔 始祖鸟 运动学 气体旋涡 翼部特点

## 1 Introduction

Over millions of years, birds have evolved ingenious morphological adaptations for different flight behaviors. Fossil birds demonstrate a number of advanced characteristics that signal evolutionary progress towards powered flight (e.g. Poore et al., 1997a). Much of our understanding of flight mechanics in birds is based on analogy with aircraft. Compared to fixed wing aircraft, however, flapping wings confer much better maneuverability and can make compensating movements to avoid stall. Birds also have the means to alter wing form to meet different flight conditions and requirements. But flexible wings require particular adaptations in the muscular and skeletal systems in order to maintain strength and high performance. Thus, to understand bird flight, we must have knowledge of wing function, kinematics, morphology, physiology, ecology and behavior.

## 2 How birds fly

Flight forces and power can be estimated adequately by lifting-line theory, but there is a range of

methods for its determination. The lifting-line model associated with vortex formation was formulated around 1910 in the Prandtl-Zhukovsky-Lanchester vortex explanation (e.g. Prandtl and Tietjens, 1934). Theoretical models for animal flight are summarized in Pennycuik (1989a), Norberg (1990, 1996), Rayner (1999), Alerstam (1990, 2000) and Spedding (1992).

In steady level flight, birds as well as aircraft must generate forces to support their weight against gravity and to provide propulsive thrust against drag. The asymmetric profile of the wing causes air to flow faster over the upper surface than underneath, so the wing experiences reduced air pressure above the aerofoil and increased pressure below. This pressure difference gives rise to a lift force,  $L$ , the magnitude of which depends on freestream velocity,  $V$ , the angle of incidence of the wing and profile shape. The total lift experienced by wings of span  $b$  is given by the Kutta-Joukowski theorem as  $L = \rho V b \Gamma$ . Circulation  $\Gamma$  is measured by the rate of rotation about the vortex lines, and can be expressed as a function of the lift coefficient  $C_{L,\Gamma} = (1/2) c V C_L$ , where  $c$  is the wing

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chord ( $c=S/b$ , where  $S$  is the wing area). This equation is described in any book on aerodynamics, such as Jones (1990) and Anderson (1991).

When a wing generates lift it also generates a system of *trailing vortices* behind the wing tips, the strength of which is determined by the magnitude of the lift force. To provide a flow of momentum matching the lift force, air must thus flow downwards behind the flying animal, creating a wing wake. Energy must be expended to generate wake vortices and also to overcome form and friction drag on both wings and body. These energy losses are experienced as drag forces  $D$ . The energy invested in the vortices is experienced as *induced drag* and can be considerable in hovering and slow flight. To reduce this component, body weight should be low and wing span long. The form and friction drag of the wings constitutes *profile drag* and that of the body is *parasite drag*. Both become increasingly important at higher speeds. To reduce the power of wing profile drag at a given flight speed, the wing area needs to be diminished; and to reduce the power of parasite drag, the body should be as slim and streamlined as possible.

A forward thrust force  $T$  must counteract the sum of horizontal components in the forces of drag. Aircraft produce thrust from engines, but a bird has no equivalent organ. In gliding flight, a bird's weight is used to counteract drag and the bird must then descend; but to fly horizontally the bird has to flap its wings so that lift has a horizontal, forward component balancing the drag. The magnitudes of lift,  $L$  and drag,  $D$ , vary with the size and shape of the wings and flight speed, and can be described by  $L=1/2\rho V^2 SC_L$  and  $D=1/2\rho V^2 SC_D$  for fixed wings, where  $\rho$  is air density. The mean lift and drag coefficients,  $C_L$  and  $C_D$ , are dimensionless numbers indicating the capacity of the aerofoil to generate lift and drag at a given angle of incidence. The lift and drag forces in flapping flight change along the wings and during the wingstroke.

The most important parameter affecting lift and drag coefficients over the entire size range of flying animals and machines is the *Reynolds number*, which is the ratio of inertial to viscous forces in air flow. The flapping wing dynamics characteristic of bird flight, which involve large-scale vortical motion, detached flows and friction, keep the Reynolds number low. In this situation, a flexible, flapping wing gives superior performance over a rigid wing (Shyy et al., 1999), providing that the wing is able to twist constantly to attain the appropriate effective angle of incidence throughout the entire stroke to produce the necessary aerodynamic forces.

### 3 Vorticity

Without wake vortices there is no momentum and thus no lift, and flight in animals and aircraft would be impossible (Weis-Fogh, 1973, 1975; Rayner, 1979a, b, c; 1995a). Vortices have three simple properties (Milne-Thomson, 1958; Pennycuik, 1989a). First, a vortex cannot end freely in the fluid: the vortex system consists of a *bound vortex* on the wing and two *trailing vortices*, one in each wake behind the wing-tips. A *transverse starting vortex* is shed whenever the strength of the bound vortex ( $\Gamma$ ) starts or changes. Secondly, circulation is conserved, so that the sum of circulations about a wing and all vortices shed into its wake is zero. Thirdly, the amount of energy needed to create a vortex is proportional to its circulation and its length. The structure of wakes has been visualized from birds flying through smoke, helium bubbles, or clouds of small particles (Magnan et al., 1938; Kokshaysky, 1979; Spedding, 1982, 1986, 1987a, b; Spedding et al., 1984). Vorticity is highly dependent on bird size, wing form, flight speed and kinematics.

In gliding flight, a pair of *line vortices* appears, as visualized in the common kestrel *Falco tinnunculus* by Spedding (1987a), whereas in hovering and slow flying birds with inactive upstroke, a series of *vortex rings* form (Kokshaysky, 1979; Spedding, 1982, 1986; Spedding et al., 1984). During hovering, kestrels perform rapid, rotational wing movements about the long axis of the wing, and the wings are only slightly flexed during the upstroke. I suggest that this rotation may be a way to build up a vortex pattern increasing the mean lift coefficient.

In faster flight with active upstrokes, when wing area is only slightly reduced during the upstroke, the wake can consist of an undulating pair of line vortices, a *concertina wake* (Spedding, 1987a). Energy is required to create transverse vortices in hovering and slow flight but not in concertina wakes. Pennycuik (1989b) suggested that concertina wakes are characteristic of birds in cruising flight, giving excellent performance in long-distance migration. He introduced the 'span-ratio' method for estimating the effective lift-to-drag ratio, based on the assumption that a bird in cruising flight is generating a concertina wake, with equal circulation in upstroke and downstroke. Pennycuik (1989a) described a fourth wake, the *ladder wake*, consisting of a combination of continuous line vortices and transverse vortices, and suggested that hummingbirds, which cannot shorten their wings in the up (back) stroke, may use this type, where the transverse vortices created change circulation at the turning points of the wingstroke.

The actual vortex system is more complicated than described above because unsteady aerodynamic factors are often significant, particularly in slow flight and hovering (Weis-Fogh, 1973; Rayner 1979b, 1995b; Spedding, 1992).

## 4 Wingbeat kinematics

Wake patterns depend on both morphology and speed and can be predicted for various *flight gaits*. Rayner (1995a) modelled upstroke lift as a function of speed, and concluded that in short-winged or slow-flying birds, the upstroke would not be used in force generation; all lift should be generated by the downstroke. In birds with relatively large wings, a lifting upstroke could become effective above a critical speed which would then initiate a transition in gait.

Tobalske and Dial (1996) found that the black-billed magpie *Pica pica*, which has short and rounded wings, does not change gait with increasing speed, whereas the rock dove *Columba livia*, which has longer wings, changes gait at 8–10 m/s. Tobalske et al. (1997) also found that, in black-billed magpies flying in a wind tunnel over a wide range of flight speeds (0–13.4 m/s), wingbeat frequency, wing-tip elevation, and relative intensity of electromyographic signals/s from the flight muscles were least at intermediate speeds and increased at both slower and faster speeds, in agreement with the theoretical U-shaped power curve (see below). Tobalske and Dial (2000) studied take-off flights in four species of Phasianidae, ranging in body mass from 0.2 to 5.3 kg, and which use flight almost solely to escape predators. All species used a similar style of wingbeat that was identified as a vortex-ring gait with a tip-reversal or supination during the upstroke.

Savings in mechanical power during flight are energetically important. Flap-gliding and flap-bounding are used by many small and medium-sized birds to save energy. Flap-gliding, which consists of flapping flight when the bird climbs and is followed by a gliding phase on extended wings, is typical of birds larger than woodpeckers and of good gliders, such as gulls and crows. During the active phase the bird must exert more power than necessary to maintain its speed so that it accelerates, and it then glides on extended wings, almost level but slowing down. Flap-bounding is used by many smaller birds, and consists of flapping phases alternating with flexed-wing bounding phases.

According to mathematical models, flap-gliding should require less mechanical power output at slow speeds (< minimum power speed  $V_{mp}$ ) than continuous flapping, while flap-bounding should require less mechanical power output at faster speeds (>

maximum range speed  $V_{mr}$ ) (Lighthill, 1977; Rayner, 1977, 1985; Ward-Smith, 1984a, b). Some birds tend to use flap-gliding when flying slowly and then shift to flap-bounding at faster speeds (Tobalske and Dial, 1994, 1996; Tobalske, 1995, 1996). Upstroke pauses also occur at intermediate and high speeds in barn swallows *Hirundo rustica*, simulating flap-gliding (Park et al., 2001). Other birds use continuous flapping during slow flight and may either change gait according to flight speed or exhibit more variation in stroke-plane and pronation angles relative to the body (Tobalske et al., 1999).

Because flap-bounding is used also in slow flight, intermittent beating may not be explained solely as adaptation to reduce power output. Its main function instead may be to increase muscle efficiency, because the muscles need rest breaks for restitution of adenosine triphosphate in the myofibrils (Pennycuik, 1989a; Oehme, 1991). Pennycuik (2001) discussed different strategies for a small bird flying near  $V_{mp}$  and suggested that, although bounding entails increased power and reduced lift-to-drag ratio, it is nonetheless an effective means of adjusting the work of muscle fibres, allowing conversion efficiency to be maximised over a wide range of speeds. Oehme (1991) showed that flap-gliding reduces the cost of transport in comparison with sustained flapping flight of equal horizontal velocity, and suggested that birds may choose to fly with equal cost of transport by varying both speed and times for flapping and gliding.

## 5 Mechanical power

Flight muscles have to do mechanical work to support body weight and overcome the form and friction drag ( $D$ ) of body and wings. The rate at which this work is done produces the *mechanical* power required to fly, which is a function of speed,  $P_{mech} = DV = MgV (D'/L')$ , where  $D'/L'$  is the inverse of the *effective* (average) lift to drag ratio. The rate at which fuel energy is required is defined as the *metabolic* power ( $P_{met}$ ). The mechanical efficiency value of the flight muscles ( $\eta$ ), which is the proportion of chemical energy converted to external work, is represented by the equation  $\eta = P_{mech}/P_{met}$  (e.g. Norberg, 1990).

The total aerodynamic power is the sum of the *induced*, *profile* and *parasite power*, due to the different drag components. The work needed to oscillate the wings, that is, to accelerate and decelerate the mass of the wings during a wing-beat cycle, represents the *inertial power* ( $\propto$  the wing moment of inertia  $I$ , where  $I \approx M_w b^2$ , and  $M_w$  is wing mass), which decreases with decreasing wing span and wing mass and increases with increasing flapping

frequency. This power component is often neglected because it is uncertain to what extent inertial power is converted into useful aerodynamic power (Weis-Fogh, 1972; Pennycuik, 1975). However, empirical data on wing lengths of birds with different flight behavior indicate that inertial costs are important in hovering and slow-flying species (Norberg, 1995a). If these costs are zero or minimal, hovering and slow-flying birds should have long wings to reduce induced power. Male birds fanning their tails in display in forward flight also benefit from elongated wings to compensate for increased parasite drag (Thomas, 1993). The shorter wings of hovering birds, including the long-tailed Jackson's widowbird *Euplectes jacksoni*, suggest that inertial costs do exist and that they may be more important in hovering and slow flight than induced power (Norberg, 1995a).

## 6 Methods used to estimate flight power

Hovering animals can be compared with helicopters, and momentum theory is often used for simple calculations of hovering force and power. Unsteady effects are significant in flapping flight and therefore the much-used simplified two-dimensional, steady-state, blade-element analysis is of limited value for calculations of induced drag and power. For these parameters, vortex theory is applied instead, while time-average steady-state aerodynamics is the tool for calculating profile and parasite drag and power. In faster flight, the variation in induced downwash is smaller; at a maximum range of speeds, induced drag and power may make up less than 10% of total drag/power. A quantitative approach, where the magnitude of the unsteady effects are estimated, provides a correction factor ( $\kappa$ ) for the estimation of induced drag and power when quasi-steady aerodynamics are used.

Physiological methods have been used to measure the metabolic power (total energy uptake) during flight (reviewed in Norberg, 1990, 1996; Rothe et al., 1987; Kvist et al., 1998; Ward et al., 1997, 1999; Nudds and Bryant, 2000). Nudds and Bryant (2000) showed that the metabolic cost of short flights in zebra finches *Taeniopygia guttata*, is at least three times the predicted value derived from models based on body mass and wing dimensions. They calculated that the metabolic cost of flight (power output) varied with body mass according to  $P_{\text{met}} = 250M^{0.87}$  for short flights and  $P_{\text{met}} = 61.7M^{0.79}$  for steady-state flights.

Both theoretical and physiological methods for measuring flight power have included diverse 'uncertain' factors, and so have often given different results. The flight cost of forward flight was estimated

by both theoretical and different physiological methods in the European starling *Sturnus vulgaris* flying in a wind tunnel (Ward et al., 1997, 1999). Measurements of total metabolic power over a range of flight speeds by both oxygen uptake and labelled isotope methods gave similar results, and showed an increase with speed in the region of around and above  $V_{\text{mp}}$ . The mechanical power for a 0.09 kg starling at  $V_{\text{mp}}$  was about 130 W/kg, and the mechanical efficiency about 0.15 – 0.18, increasing moderately with flight speed (Rayner, 1999). Heat transfer, measured by infrared thermography, confirmed the estimates of efficiency (Ward et al., 1999).

An alternative method has measured force directly from the flight muscles by implanting a strain gauge on the deltoid crest of the humerus, at the insertion of the pectoral muscle. Such studies have been carried out on a starling in a wind tunnel (Biewener et al., 1992), and on a rock dove *Columba livia* (Dial and Biewener, 1993) and a black-billed magpie *Pica pica* (Dial et al., 1997) in free flight. The distance shortened by the muscle, estimated from video recordings, was multiplied by the measured force to give the work done in each contraction; multiplying this by wingbeat frequency gave mechanical power output. But Pennycuik et al. (2000) noted that the estimates are proportional, rather than equal, to the actual work done, because the force and distance shortened are not definable in the pectoral muscle due to rotational movements (see below), and because different fibers in the muscle shorten through very different distances. Instead of measuring muscle force and distance shortened by the muscle, Pennycuik et al. (2000) recorded the moment exerted by the muscle and the angle through which the humerus rotates in the barn swallow *Hirundo rustica*. The work done by the pectoral muscle was obtained by multiplying the moment by the angle, from which average mechanical power was then calculated. This direct method will be improved further and applied to a range of species (Pennycuik et al., 2000).

## 7 Power versus speed curve

The theoretical mechanical power versus speed curve is necessarily U-shaped (Pennycuik, 1968). Its bottom point defines the *minimum power* and *minimum power speed* at which a bird can fly for the longest time on a given amount of energy; and the tangent to the curve defines the *maximum range power* and *maximum range speed* for maximization of flight distance on a given amount of energy. If basal metabolic rate  $P_b$ , the circulation and ventilation factor (often labelled  $k$ ) and flight muscle efficiency  $\eta$  are independent of speed, then the metabolic

power curve will take the same U-shape form as the curve for mechanical power. But, most probably, this is not so. Comparisons of measured metabolic power and computed mechanical power suggest that flight efficiency increases with bird size (Rayner, 1995b, Norberg, 1996), and it may also increase as flight speed increases (Rayner, 1979b). This may explain why some metabolic curves of birds in flight, based on respirometric measurements of oxygen consumption, have usually shown that power has little dependence on speed, giving almost flat, or slightly J- or L-shaped graphs (e.g., Ellington, 1991; Djal et al., 1997). But it was found to be U-shaped in the budgerigar *Melopsittacus undulatus* (Tucker, 1968) and slightly U-shaped at the measured medium speeds in the rock dove (Rothe et al., 1987). Moreover, recent physiological evidence suggests that the chemical power curve even is more strongly U-shaped than predicted by Pennycuick's (1989a) physical model (Kvist et al., 1998).

Because the sum power-curve depends on three power components, variations due, for example, to different theoretical models applied to those components will change the settings for minimum power and maximum range speeds, and for the related minimum and maximum powers. The body drag coefficient, for example, ranges with different estimates from 0.07 to 0.77 for small birds (Pennycuick, 1989a; Pennycuick et al., 1988; Tucker, 1990, 2000; Hedenström and Liechti, 2001). Pennycuick (2001) and Tucker (2000) now suggest that  $C_{Db} = 0.1$  should be used as a reasonable value for birds of different sizes.

Thomas (1996a, b) used a simple aerodynamic model to examine the effect of the tail and variable wing geometry on the power required for flight. To minimise power at low speeds, the wings and tail should be spread widely, but at higher speeds, wing span and area should be reduced instead to minimize the power required for flight. The interaction between wings and tail can also reduce induced drag in slow flight most effectively (Thomas, 1996b). As speed increases, the angle of attack of the tail should be gradually reduced until completely furled. When the tail is included in power calculations, the shape of the power curve becomes dependent on bird morphology (Thomas, 1996a). The power curve is then W-shaped for birds with a large forked tail, with one local minimum at a low speed when the tail is spread, and one at a higher speed when the tail is furled.

It is thus extremely difficult to determine an accurate shape for the power curve of flapping flight, particularly at high flying speeds. It may therefore be unrealistic to compare measured flight speeds in birds with optimal speeds estimated from theoretical

power curves (see Pennycuick, 1997). A number of publications have considered the issue of air speeds that minimize either energy consumption or flight time during migration (e.g., Hedenström and Ålerstam, 1995; Ålerstam and Hedenström, 1998; Ålerstam, 2000). To cope with this problem, Pennycuick (2001) established physical 'benchmarks' against which the flight performance of wild birds could be measured, without influence from any hypothesis about the flight speeds at which birds should be expected to fly. He measured air speeds and wing-beat frequencies, and then compared them with benchmark values computed by his modelling program (Pennycuick, 1989a).

## 8 Gliding and soaring

In gliding flight, the muscles do not provide any power other than to keep the wings outstretched and for correcting maneuvers; only potential energy is used up. The costs for gliding flight during migration have been estimated as approximately 3–4 times the basal metabolic rate (Hedenström, 1993). The aerodynamics, performance and behavior of gliding and soaring flight have been thoroughly investigated in a variety of birds by, among others, Pennycuick and Tucker with their colleagues (for references, see Pennycuick, 1989a; Tucker, 1998, 2000; Rosén and Hedenström, 2001). As in the case of flapping flight, estimations of the body drag coefficient are important for assessments of gliding. Stability in gliding flight is discussed by Thomas and Taylor (2001).

Albatrosses and petrels are the dominant flying birds of open ocean in the southern hemisphere. They soar often and consistently. Based on their flight, the classical theories of 'dynamic' soaring (reviewed in Tickell, 2000) concluded that gliding flight could be sustained in horizontal wind by a gradient that increased in strength with height (Cone, 1964). But whereas albatrosses typically rise to around 15 m in their gliding before pulling out, Pennycuick (2002) performed a simple calculation showing that wind gradients strong enough to sustain soaring could only be expected up to a height of about 3 m above the surface of the sea. Pennycuick went on to propose that the birds do not extract energy from the horizontal motion of the wind relative to the water surface, but instead extract pulses of energy from discontinuities in the wind flow ('gusts') due to flow separation over wave crests. Pennycuick further suggested that the forward-pointing nostrils of procellariiform birds serve as pitot tubes and that their large nasal sense organ can monitor dynamic pressure. Petrels and albatrosses may thus have the sensory ability to take advantage of energy in the gusts. Birds

flying with flapping flight or taking advantage of slope soaring along swells, such as gannets and boobies, do not have such nostrils.

## 9 Scaling of flight parameters

Empirical allometric relationships allow exploration of how different mechanical, physiological and ecological constraints change in importance with size and wing form (see, e. g., Greenewalt, 1962; Rayner, 1988; Norberg 1990, 1996; Tennekes, 1996; Shyy et al., 1999). The lift equation given above (section 2) shows how body weight, wing area, air density and air speed are connected. It is clear that cruising speed depends on *wing loading*, where  $Mg/S = \rho V^2 C_L / 2$ . Maneuverability also depends on wing loading, because minimum radius of turn  $r$  in a balanced turn is directly proportional to wing loading, viz.  $r \propto Mg/S$ . Wing loading increases with the size of the bird (for geometric similarity,  $Mg/S \propto M^{1/3}$ ), which has an influence on flight performance.

*Aspect ratio* is a non-dimensional number reflecting the shape of the wing; it is defined as the ratio of wing span to mean chord  $c$  and calculated as  $AR = b^2/S$ . In geometrically similar birds, aspect ratio is constant. It can give indications of flight characteristics: agility and maneuverability improve with smaller aspect ratio, whereas the lift-to-drag ratio (= glide ratio) increases with increasing aspect ratio. Aerodynamic performance can be improved by making the wings longer and thinner, thus increasing the aspect ratio as is done in modern sailplanes. At a constant angle of attack this reduces the lift coefficient. The longer the wings, the smaller the wing-tip vortices, with decreased induced drag and power as result. This is important for slow flying species in which induced drag is a dominant component of total drag. But very long wings are more vulnerable to breakage and can be of hindrance in a cluttered environment and take-offs from the ground.

*Wingbeat frequency* at maximum depends on the force exerted by the muscle in question and the length of the bone that is moved. Pennycuik et al. (1996) used a combination of multiple regression and dimensional analyses on empirical data for 47 morphologically diverse bird species to show that *natural* wingbeat frequency may be estimated by:  $f = (Mg)^{1/2} b^{-17/24} S^{-1/3} I^{-1/8} \rho^{-3/8}$ , where  $I$  is wing moment of inertia ( $I \sim M_w b^2$  and  $M_w$  is wing mass). This equation predicts that if, for example, the body mass were to change in the course of a flight in one individual (at the same air density), this should cause wingbeat frequency to change in proportion to the square root of body mass (see also Pennycuik et al., 1996). Predicted wingbeat frequency can be

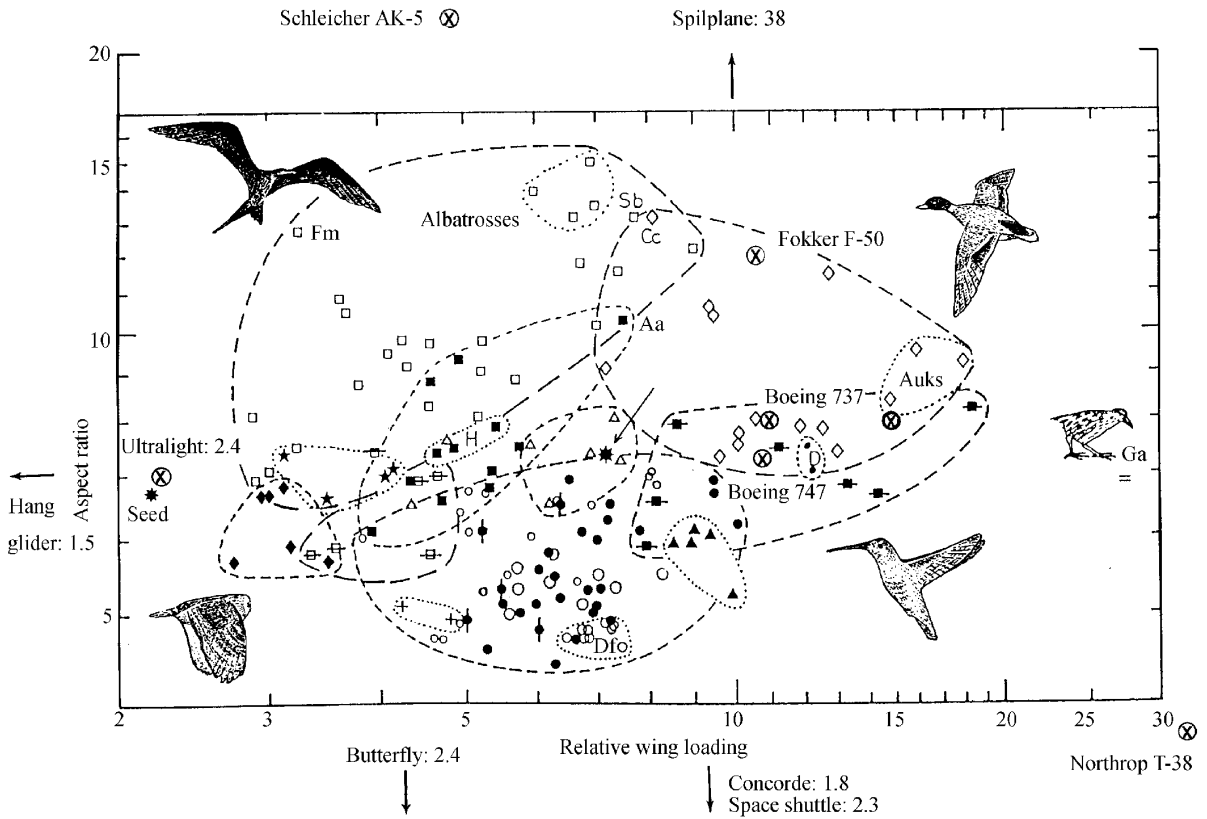
used to estimate the mechanical power required to fly, for the mechanical power produced by a particular flight muscle is directly proportional to its frequency of contraction (Hill, 1950). Liechti and Bruderer (2002) found that house martins *Delichon urbica*, and barn swallows *Hirundo rustica*, had lower wingbeat frequencies in free flight than in wind tunnel experiments.

The maximum load that a flying animal can lift during take-off has been shown to be proportional to body mass over a broad range of body sizes (Marden, 1994); thus mass-specific lifting ability is independent of body size. For geometrically similar animals, Marden's (1994) multivariate regression indicates that lift per unit muscle power scales with body mass as  $M^{-0.16}$ , which means a decline in flight ability with increasing body mass. Tobalske and Dial (2000) used whole-body kinematics from four species of the Phasianidae to estimate that the take-off power (the excess power available for climbing and accelerating in flight) scaled with body mass as  $M^{0.62-0.75}$  and that pectoralis mass-specific take-off power decreased in proportion to  $M^{(-0.33)-(-0.26)}$ , directly proportional to wingbeat frequency. They also found that muscle strain  $\epsilon$  increased with body mass as  $M^{0.23}$ , but that there was no significant correlation between stress  $\sigma$  and body mass. Askew et al. (2001) estimated the mechanical power output of a quail during take-off to be about 390 W/kg. In four other species in the family Phasianidae, moreover, Askew and Marsh (2001) found no significant scaling of mass-specific power output with body mass in take-off, but that there was a tendency for power to decrease in the largest species in proportion to  $M^{-0.14}$ .

## 10 Wing and tail form and flight mode

Different combinations of wing loading and aspect ratio permit an aircraft or flying animal to adopt particular flight modes and foraging strategies (Rayner, 1988; Norberg and Norberg, 1989). Fig.1 shows aspect ratio along the y-axis and a mass-compensated measure of wing loading ("relative wing loading") along the x-axis of extant birds *Archaeopteryx*, some aircraft, a hangglider, a butterfly and a seed. Powered aircraft are not limited by power requirements in the same way as animals, and have values outside those for animals which have to beat their wings to produce thrust (Lindhe Norberg, 2001). It is thus more appropriate to compare gliding vehicles with gliding and soaring in animals.

*Wing form.* Birds with long, high-aspect-ratio wings also have low wing loadings, in particular those with low body mass; and their flight is correspondingly slow and inexpensive. Such species nor-



**Fig.1 Aspect ratio versus wing loading index (independent of body size) in some birds, *Archaeopteryx*, airplanes, a hang-glider, an ultralight, a butterfly and a maple seed**

Ga=*Gallirallus australis*. Numerals against objects refer to aspect ratio. Data for aircraft are from Tennekes (1996). Figure adapted from Lindhe Norberg, 2002, by courtesy of Wiley-Liss, Inc. (modified from Norberg and Norberg, 1989).

mally use continuous foraging and cruising flights in open spaces, and include many seabirds and the swifts and swallows. Wing-tip shape varies among the species, which affects the mode of flight, but the size of the aspect ratio still gives an indication of flight energy costs as well as maneuverability. Swifts and ocean birds that soar over long distances have high-aspect-ratio wings with highly tapered aft-swept tips. This lunate-shaped lifting surface can extract more energy from the vortical wake and produce less drag for given lift than lifting surfaces with an elliptic circumference of the kind that occurs in more rounded wings (van Dam et al., 1993).

Birds flying among vegetation, such as many owls and small passerines, are usually perchers. Ultralight aircraft resemble owls. The low aspect ratios in owls contribute to high induced drag, but on the other hand their low weight and large wing area, and thus low wing loading, aid in decreasing flight costs. Small passerines with low aspect ratios spend much of their foraging time walking, climbing, clinging and hanging. Low wing loadings and low aspect ratios are beneficial for maneuverable flight. In contrast, species with high wing loadings and short wings but

still of high aspect ratios, are adapted to fast and rather expensive flight and their maneuverability is low. Commuters and migrants are found among such species, for example loons, grebes and waterfowl. Auks have lower aspect ratios and still more costly flight.

There are not many flying species that combine a high wing loading with a low aspect ratio, which requires the highest energy costs for flight. Gallina-ceous birds belong to this category. Birds with still higher wing loadings have lost the ability to fly, such as penguins, ratites and several rails. Humming-birds, which are excellent hoverers and maneuverers, are close to gallinaeous birds in this scheme; but they use different flight kinematics than other birds, and represent extremes of locomotor and metabolic capacity among the vertebrates (e.g. Weis-Fogh, 1972; Norberg, 1990; Altshuler and Dudley, 2002). The wing dimensions of *Archaeopteryx* were about the same as those of modern pigeons and some waders; its relative wing loading was about average for extant species and its aspect ratio slightly higher. Many species in this category forage on the ground and in water.

Migratory birds should have long wings of high aspect-ratio for enduring flight and to cover as great a distance as possible on a given amount of energy (Pennycuik, 1989a). Such wings are of rather large area, giving a low wing loading. However, migrating birds that need both sustained and fast flight benefit from both a high aspect ratio and a high wing loading, although this combination is theoretically more costly (Norberg, 1995b). Many migratory birds, nevertheless, do not have to fly fast, and several of them have rather low wing loadings. The mean aspect ratios for long-distance migrants, short-distance migrants, and partial migrants are 8.2, 7.4, and 5.5, respectively (Norberg and Norberg, 1989; Norberg, 1995b). The two migratory groups differed significantly from the partially sedentary group, but not so much from one another. In contrast, relative (size-independent) wing loading is significantly higher in short-distance migrants than in long-distance migrants and partial migrants, which do not differ significantly from each other.

*Tail form.* The tails of birds vary far more than their wings. Although the tail reduces overall lift-to-drag ratio, it is nevertheless important in maintaining stability over a range of flight speeds (Norberg, 1990) and in generating lift to help in turning and slow flight (Thomas and Balmford, 1995). In slow flight and maneuvering, the tail is usually spread to maintain stability and balance and to generate lift additional to that of the wings (Tucker, 1992; Thomas, 1993; Norberg, 1994). Open-country birds selected for high lift-to-drag ratios have relatively short tails, whereas birds that need high maneuverability in order to feed aerially or avoid collisions in cluttered environments have longer tails (Thomas and Balmford, 1995).

Many birds have a tail in which the outer rectrices are longer than the inner, so that when spread, the tail takes on the shape of a 'delta wing'. Thomas (1993) applied slender lifting surface theory to a bird's tail, the entire lifting surface of which was interpreted as effectively equivalent to the wing-tips of a conventional high aspect-ratio wing. This theory has been used to model delta winged aircraft, such as the concord, and has been tested by the aerospace industry. According to it, air flow over the tail is three-dimensional, with transverse flows moving around the leading edges from below to the dorsal surface. The model shows that the lift generated by the tail is unaffected by its shape but proportional to the square of its continuous span. Only that part of the tail in front of the point of the maximum width of the spread tail is aerodynamically functional, and any area behind this point will cause drag due to friction. Therefore, any tail with highly elongated inner

feathers like those in sexually dimorphic species, will add considerably to the cost of flight (Norberg, 1995a), in contrast to the outer tail streamers in the barn swallow, which Norberg (1994) showed produced lift and increased maneuverability during flight.

*Wing span, wing area, tail spread, and tail angle of attack* can change substantially during a wingbeat, and the geometry of the lifting surfaces adopted during maneuvers or accelerating in flight can differ substantially from that in steady flight. Variations in such geometry are correlated systematically with flight speed; the tail can reduce the power required for flight at low speeds, and a shortened wing span can reduce it at high speeds (Thomas, 1996a). This is observed also in gliding birds (e.g., Pennycuik, 1989b; Tucker, 1992; Rosén and Hedenström, 2001).

*Costly modes of flight* are often exemplified in display flight associated with sexual selection (e.g., Norberg, 1991). Males evolve special traits, for example a long tail, which is used by females as an indicator of quality to guide mate choice (M. Andersson, 1982, 1994; S. Andersson, 1992). To compensate for the increased drag from a long tail, such males should fly slower than short-winged species of otherwise similar size, and they should have larger wings (lower wing loadings) to reduce the overall power required to fly (Norberg, 1995a). Evans and Thomas (1992) also predicted that such birds should have longer wings, which corresponds well with the relationship between tail length and wing length observed.

*Moulting* in birds is energetically costly, because it reduces aerodynamic performance (Thomas, 1993; Swaddle and Witter, 1997; Hedenström and Sunada, 1999), increases the energy cost of thermoregulation, and draws on body resources for synthesizing new feathers (reviewed in Lindström et al. 1993).

*Unsteady aerodynamics and lift-enhancing characteristics.* Flapping flight always includes phases with unsteady air flow, which can take the form of intense local vortices shed from the leading edge of the wing or wing-tips, or vortices trapped on or close to the wings (Spedding, 1993; Rayner, 1995a). When the Reynolds number decreases, unsteadiness in the freestream velocity becomes more significant, and the lift-to-drag ratio decreases. A main problem for flying animals and aircraft is therefore to gain enough lift in slow flight. By employing unsteady mechanisms, flapping birds can overcome deteriorating aerodynamic performance under steady flow conditions at low Reynolds numbers (Shyy et al., 1999). This is important during take-off and land-



ing, and also for many birds that take prey in the air or fly among vegetation.

Lift can be increased by increasing the camber (anteroposterior curvature) and/or the angle of incidence of the wings, though at the expense of increased drag. If the camber or angle of incidence becomes too great or the speed too low, the air becomes turbulent over the wing, creating a sudden fall in lift and increase in drag; and the wing stalls. Although this is disastrous for aircraft, a bird can usually control its flight even after stalling accidentally. Stalling can be delayed or avoided by *high-lift devices*, such as flaps and/or leading-edge slats, that increase the maximum lift coefficient above that for the reference aerofoil itself. High-lift devices thus allow aircraft- and flying birds- to fly slower while still generating enough lift to balance their weight. Various flap concepts are described in Norberg (1999) and Lindhe Norberg (2001).

### 11 Maneuverability and agility

Birds perform aerial maneuvers in different ways depending on the purpose, whether catching prey, displaying, avoiding obstacles or landing. Norberg and Rayner (1987) defined *maneuverability* in terms of the minimum radius of turn that a flying animal can attain, and *agility* as the maximum roll acceleration during the initiation of a turn, i.e. the ease or rapidity with which the flight path can be altered. To initiate a turn, a net rolling moment must be produced, and this can be done by differential twisting or flexing of the wings, or by flapping the two wings unequally so that the aerodynamic roll moments of the two wings become asymmetrical (Norberg and Norberg, 1971; Norberg, 1976, 1990; Warrick and Dial, 1998). Taylor and Thomas (2002) suggested that an active upstroke could be used to lower stability and enhance maneuverability.

Because the radius of a banked turn is proportional to the square root of the wing loading, the highest maneuverability is attained by small birds with large wings (Fig.2). The aerodynamic roll moment (torque)  $M$  is proportional to the speed squared, wing area and wing span,  $M = (1/2) \rho C_{m} V^2 S b$ , where  $C_m$  is the coefficient of roll moment (Norberg and Norberg, 1971; Thollessen and Norberg, 1991).  $C_m$  is influenced by wing shape and will be greatest on large wings with broad, rounded tips. Thus, at a given speed, long broad wings with rounded tips will provide large aerodynamic torque and hence high agility. Large torque can also be obtained by high speeds, but high speeds do not agree with large wings of low wing loading. Therefore, low torque  $M$  is obtained by the large size role is in high-velocity rotation of the humerus,

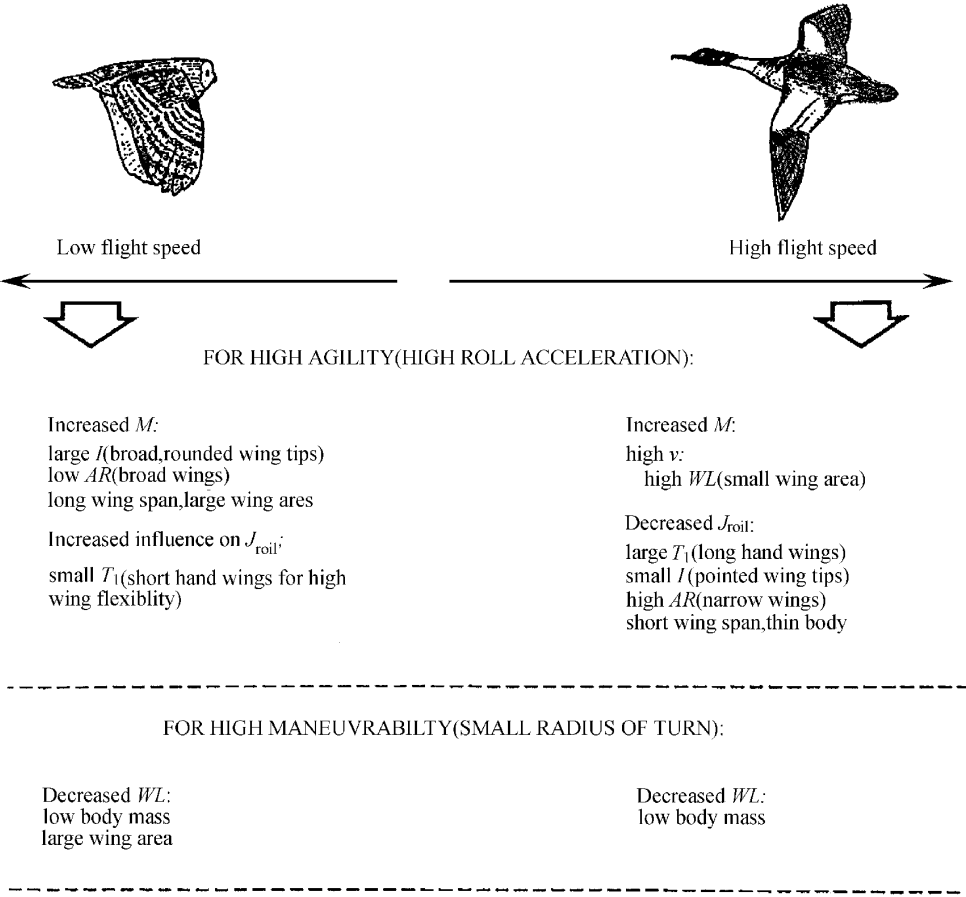
of wings in slow-flying species and by high speeds in fast-flying species.

Furthermore, the fastest entry into a turn is achieved at the maximum angular acceleration,  $\alpha_{roll}$ , available to a bird, which equals the aerodynamic torque divided by the total roll moment of inertia ( $J_{roll}$ ) of body and wings,  $\alpha_{roll} = M/J_{roll}$  (Andersson and Norberg, 1981). To enhance rapid maneuvers, a bird should thus provide a large torque and/or a small roll moment of inertia. Kirkpatrick (1990) found in a sample of birds that the wing moment of inertia, scaled with body mass as  $J_{roll} \propto M^2$ , and with wingspan as  $J_{roll} \propto b^5$ . To produce a small rolling moment of inertia the bird should thus be small and have short wings. Therefore, in slow-flying species *broad wings* and *wide tips* are important for high agility (by maximizing the torque), whereas in fast-flying species *a thin body*, *short wings* and *pointed wing-tips* provide a small roll moment of inertia (Thollessen and Norberg, 1991; Fig.2).

### 12 Feathers, flight muscles and skeletons

The animal body is usually subjected to more varying loads than man-made structures. For flight, then, birds have evolved diverse morphological adaptations for leverage and elasticism in their skeletal and muscular systems. Feathers are extremely light and elastic structures (Bonser and Purslow, 1995; Corning and Biewener, 1998), and those of the wing tip probably store and release energy at the bottom of the wing stroke (Pennycuik and Lock, 1976). Moreover, although the vanes of body feathers are mainly symmetrical, those in the wings that are used for flight (remiges), and the lateral tail feathers, are strongly asymmetric. The remiges are also curved. Their structural asymmetry is essential for their bending and twisting throughout the wing-beat cycle; the angles of attack of the feathers are adjusted automatically to continuously varying directions and velocities of the wind passing over them (Norberg, 1985). Norberg showed that the inherent aeroelasticity of wing feathers is achieved by a combination of three traits, namely vane asymmetry with increasing asymmetry towards the feather tips, shaft curvature, and unequal flexural stiffness which is greater dorsoventrally than anteroposteriorly. Vane asymmetry also occurred in *Archaeopteryx* (see below).

The main downstroke muscle, the pectoralis, is structurally and functionally complex (reviewed in Goslow, 1991). Although the supracoracoideus muscle is capable of elevating the humerus, its primary which may also serve to augment supination of the



**Fig.2 Theoretical selection pressures for high agility (= high roll acceleration) and high manoeuvrability in fast-flying and slow-flying birds**

$\alpha_{roll} = M/J_{roll} \propto vSb/J_{roll}$ , where  $M$  is the torque,  $v$  is flight speed,  $S$  is wing area,  $b$  is wing span and  $J_{roll}$  is the roll moment of inertia of body and wings combined.  $I$  is wing-tip shape index and  $T_1$  is wing-tip length index (Norberg and Rayner, 1987),  $AR$  is aspect ratio and  $WL$  is wing loading (modified from Tholleson and Norberg, 1991).

wrist during the upstroke (Poore et al., 1997a, b; see also Ostrom et al., 1999). Sokoloff et al. (2001) reported that the common starling *Sturnus vulgaris* is still capable of ground-level take-off after denervation or tenotomy of the supracoracoideus muscle. In such circumstances, there was an increase in activity of the deltoid complex as well, together with strong leg thrust.

Pneumatic bones that reduce weight characterize most birds: hollow bones achieve a given strength/weight ratio better than solid ones. The U-shaped furcula (clavicles) in birds also acts as a spring, bending laterally during the downstroke, thereby storing elastic energy which may be used when recoiling during the upstroke (Jenkins et al., 1988; Goslow et al., 1989). Goslow et al. (1989) suggested, however, that the main function of furcular movements is to facilitate breathing. The avian wrist shows extraordinary adaptations for flight (Vazquez, 1992, 1994). Vazquez (1992) investigated the morphology of the avian carpal-metacarpal complex and demonstrated how the articular surface of the

trochlea carpalis acts to automatically supinate the hand upon wrist flexion. In *Archaeopteryx*, the semilunate carpal (a precursor of the trochlea carpalis) may have served for automatic supination of the hand and metacarpus (Vazquez, 1992; Ostrom et al., 1999).

### 13 Evolution of bird flight

Since the 1984 International *Archaeopteryx* Conference in Eichstätt, Germany (Hecht et al., 1985), many new birds have been described from the early Cretaceous of China (e.g., Zhang and Zhou, 2000; Zhou and Zhang, 2001a, b, 2002; Zhang et al., 2001). These lend new insights into the understanding of the evolution of birds and bird flight, and of the flight capabilities of ancient birds. Early Cretaceous birds were the first to have a keeled sternum, a strap-like coracoid, and hypocleidium-bearing furcula, structures that are characteristic of modern birds.

Whether birds evolved flight via gliding, starting from some height or slope and working with grav-

ity (the “trees-down” theory), or from a terrestrial running ancestor working against gravity (the “ground-up” theory), is still intensely debated. Several suggestions modifying the various evolutionary steps in the main theories have also been put forward, laying stress on whether a gliding stage was included or not. Various aspects of the life style of early birds were discussed in the 2001 International Symposium in Honor of John H. Ostrom in New Haven, Connecticut, in 1999 (Gauthier and Gall, 2001). Burgers and Padian (2001) proposed that running proto-birds received lift from the *ground effect* when flapping their wings extensively to produce thrust. The main benefit from flying close to the ground is a savings in induced drag and a reduction in the thrust needed for level flight, as well as, at slow flight speeds, an increase in lift. O’Farrell et al. (2002) suggested that *Archaeopteryx* relied substantially on lift enhanced by ground effect.

In terms of energy, time, and aerodynamics, the gliding hypothesis is an attractive alternative (Norberg 1985a, b, 1990), but arguments have been raised about structural limitations in early proto-birds. Rayner (2001) nevertheless demonstrated that the evolution of powered flight through a gliding wing is entirely consistent with the existing fossil record, and that this hypothesis makes few demands on the behaviour and paleobiology of proto-avians. With a detailed mathematical model, I have shown that a transition from parachuting and gliding to active flight is mechanically and aerodynamically feasible. By using aerodynamic and optimal foraging theories, I showed that for every step along the hypothetical route from gliding, through stages of incipient flapping, to fully powered flight, there would have been an advantage over previous stages in terms of length and control of the flight path (Norberg, 1985a, b, 1990). Asymmetric wing movements would first have been used for slight maneuvering to correct glide paths. Later, a slight flapping was used for the initial production of thrust.

Burgers and Chiappe (1999) and Burgers and Padian (2001) proposed that the generation of thrust, not lift, was of paramount importance in the origin of bird flight. But this is indeed the most important point in my own detailed aerodynamic model, namely that *thrust* is produced in a gliding animal with slight flapping, concerning which Rayner (1985) also pointed out in a graph that thrust had to be produced during gliding to flatten out the glide path. I showed that a net thrust force can be produced even during very slight flapping in a gliding animal while the necessary vertical lift is still produced, resulting in a shallower glide path (Norberg, 1985a). Furthermore, an animal (or aircraft) can-

not fly unless it produces a lift force to counteract gravity; and the simplest way for a proto-bird with small primordial wings to obtain lift is to use parachuting/gliding from a height.

My estimation for a proto-bird the size of *Archaeopteryx*, with a gliding speed of about  $7 \text{ m s}^{-1}$ , wing beats about ten times faster in the downstroke than upstroke, and an almost vertical stroke plane ( $9^\circ$ ), gives a *net thrust* that would be produced by a wingstroke frequency as low as  $2 \text{ s}^{-1}$  (Norberg, 1985a). In fact, I have observed such unusual flapping behaviour in the red-tailed cockatoo *Calyptorhynchus banksii* in northeast Australia. Furthermore, my model shows that wingstroke amplitude increases almost linearly with flapping speed and that it is small at low speeds.

## 14 Did *Archaeopteryx* fly?

Whether *Archaeopteryx* was capable of powered flight or only an advanced glider is not a simple question to answer. *Archaeopteryx* seems to lack a morphologically derived supracoracoideus muscle that would produce a rapid humeral rotation; and the skeletal features associated with it, an acrocoracoid, a triosseal canal, and a tuberculum dorsale, were apparently incapable of high-velocity rotation of the humerus about its longitudinal axis during the upstroke (Ostrom, 1976; Wellnhofer, 1988, 1993; Jenkins, 1993; Poore et al., 1997a, b; Ostrom et al., 1999). However, the presence of a semilunate carpal, a reptilian character, may have served for automatic supination of the hand and metacarpus (Vazquez, 1992). A well-developed scapula and acromion process, and an enlarged humeral deltopectoral crest, indicate that the deltoid muscles were well developed, and these instead may have worked to elevate the wings (Ruben, 1991). The glenoid underwent a major reorientation during the evolution of the avian shoulder, from a primitive posterioventrally-directed condition to the dorsolaterally-directed state found in modern birds. The laterally facing glenoid of *Archaeopteryx* was intermediate in orientation, and provided for a substantial degree of wing elevation even if not as great as in modern birds (Jenkins, 1993).

The absence of a sternal crest and a calcified sternum, the presence of a simple pectoral girdle similar to that of nonflying theropods, and a lateral-facing glenoid, indicate that the downstroke of *Archaeopteryx* was rather weak and dorsoventral, and with little pronation (Rayner, 2001). Given its inability to produce a rapid upstroke with supinated wings and that its downstroke was poor and dorsoventral, Rayner concluded that *Archaeopteryx* was incapable of slow flight and better for fast cru-

ing flight, with little agility and maneuverability.

The remiges of *Archaeopteryx* had stiffened rachis (Rietschel, 1985) and showed vane asymmetry (Feduccia and Tordoff, 1979). Norberg (1985) showed that *Archaeopteryx* had the structural asymmetry of remiges that, as in modern birds, is essential for automatic adjustment of the feathers for optimal angle of incidence throughout the wing-beat cycle. This indicates that *Archaeopteryx* could have been a relatively advanced flier, although it has to be said that its remigial characteristics would also be beneficial for a maneuverable glider. Even so, it seems unlikely that the remiges would have been so strongly curved if *Archaeopteryx* had been just a glider (Norberg, 1985). Feather asymmetry is highly beneficial for both maneuverability and flapping flight, which evolved step-by-step and most probably simultaneously with one another (Norberg, 1985a, 1990). Furthermore, *Archaeopteryx* had a relative wing loading and aspect ratio similar to the “average” modern bird (Norberg, 1990; Fig.1).

So *Archaeopteryx* may have been able to use weakly powered cruising flight with some manoeuvrability. A ladder or concertina vortex wake may have been produced during flapping, which were probably intermediate in form between line vortices and vortex rings in the evolution of flight (Norberg, 1985a).

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## Evolutionary dynamics of sympatric Darwin's finch populations in the Galápagos Archipelago \*

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**Abstract** The focus of this paper covers three stages in the speciation cycle: colonization, lineage divergence and reproductive isolation. It begins with an investigation of divergence through time, then examines the nature and robustness of the barrier to gene flow between populations, and ends with a description of a founder event that gives insight into the colonization process. The work is part of a long-term study into the evolution of Darwin's Finches on Isla Daphne Major, Galápagos, carried out by Peter Grant, colleagues and myself. This radiation is young; all 14 species alive today are estimated to have been derived from a common ancestor approximately 2 to 3 million years ago. Extreme inter-annual fluctuations in climate alter the ecological conditions and food supply for the finches. Populations were found to track these changes through repeated evolutionary responses to natural selection events. The cumulative effect across a 30 year period was a significant change in mean body size and beak shape in populations of both *Geospiza fortis* and *G. scandens*. Song, a culturally transmitted trait learned early in life by an imprinting-like process, acts as a reproductive barrier between these species. However this barrier leaks as a result of rare incidences of misimprinting on song, which can lead to hybridization and introgression under some ecological conditions but not others. The trickle of genes flowing from one species to another increases genetic variation on which selection can act. In 1983 the large ground finch *G. magnirostris* colonized Isla Daphne Major. The population began with two brothers and a sister mating in different combinations. New immigrants to the island later supplemented this inbred population and today numbers are close to 50 breeding pairs. These results have two implications. The first is that interaction between ecology, genetic and learned behavior is important in speciation. The second is that neither environments nor species are static entities; and if we are to conserve them, they must be kept capable of further change [*Acta Zoologica Sinica* 50 (6): 936–941, 2004].

**Key words** Speciation, Hybridization, Imprinting, Reproductive Barrier, Founder Event, Darwin's Finches

## 加拉帕戈斯群岛同域达尔文雀种群的进化动态 \*

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**摘要** 本文主要论述物种形成的三个阶段: 建群、线形分异和生殖隔离。首先介绍一项通过时间产生分异的调查, 然后检测种群间基因交流的障碍, 最后描述一个自然事件从而分析建群过程。本项工作是在加拉帕戈斯群岛中的达芬梅杰岛上长期研究达尔文雀进化工作的一部分, 研究组成员由格兰特、笔者和其他同事组成。岛上发生适应辐射的时间并不长, 现存的 14 种达尔文雀由 200 或 300 万年前的一个祖先分化而成。极端的年间气候波动改变了达尔文雀的生态条件和食物供给。达尔文雀种群受到这些变化的影响, 通过重复的进化反应, 发生了自然选择。通过 30 年的积累, 中地雀 (*Geospiza fortis*) 和仙人掌地雀 (*G. scandens*) 种群的体型大小和喙部形状发生了显著的变化。达尔文雀的鸣叫是在幼鸟时期通过学习而形成的, 类似于印痕过程, 鸣叫对保持种间的生殖隔离起着一定的作用。但是在一些特殊的生态条件下, 生殖隔离可以被由于错误印痕所形成的鸣叫而冲破, 导致种间杂交和基因渗入, 当然, 这种情况非常罕见。自然选择可以使基因流从一个物种流动到另一个物种从而增加变异。1983 年, 大地雀 (*G. magnirostris*) 在达芬梅杰岛上建群。最初岛上只有拥有共同亲鸟的 2 只雄鸟和 1 只雌鸟通过不同的配对关系维持着种群。后来新迁来的地雀补充了这个近亲繁殖的种群, 目前岛上已有近 50 对大地雀。这个现象给我们两点启示: 一是生态、遗传和学习行为的相互作用在物种形成过程中至关重要; 二是物种和环境都不是静止不动的, 如果我们要保护它们, 必须使它们保持进一步变化的能力 [动

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关键词 物种形成 杂交 印痕 生殖屏障 奠基者事件 达尔文雀

1 Introduction

More than sixty years ago, Mayr (1940) and Dobzansky (1940) identified lineage divergence and the formation of a reproductive barrier between lineages as important stages in species formation. Yet questions are still raised concerning the role of history, geography, and genetic variation in lineage divergence (Givinish, 1998); the relative roles of genetic variation (Wu, 2001) / behavior and learning as factors in the formation of reproductive barriers (ten Cate and Voss, 1999); and the genetic changes occurring during colonization events (Slatkin, 1996; Charlesworth, 1997; Templeton, 2001).

Young adaptive radiations of birds on isolated island archipelagos are suitable systems for investigating all three stages of speciation—colonization, lineage divergence and formation of reproductive barriers, because all species are recently derived from a common ancestor and populations of closely-related species occur together or separately on different islands. Such a situation allows measurements of lineage divergence across space when populations of the same species occur on ecologically different islands, and through time when climatic changes alter the ecology of an island. It also allows investigation into the nature and strength of reproductive barriers between closely-related sympatric species. Furthermore, founder events occur frequently in archipelagos, and, if witnessed, can be tracked to give insight into the process of colonization. Thus these three major steps in the process of speciation can be investigated during contemporary time.

The radiation in Darwin's finches (*Geospiza*, *Camarhynchus*, *Certhidea* spp.) on the Galapagos Archipelago is young. Mitochondrial DNA data suggest that the finches are derived from a Tiaris-like ancestor that arrived on the islands from the American mainland 2 to 3 mya (Sato et al., 1999, Petren et al., 1999; Grant and Grant, 2002a). Today 13 of the 14 species of Darwin's finches occur on islands throughout the archipelago, the fourteenth being on Cocos Island 600 km to the northeast. This radiation has two further advantages for studies in speciation. First, many islands are in pristine or near pristine condition and no species of finch has gone extinct as a result of human interference, unlike the situation in Hawaii (Freed et al., 1987) and Madagascar (Yanaguchi et al., 2001). Secondly, the archipelago sits astride the equator and is subject to extreme

inter-annual climatic fluctuations caused by the El Niño Southern Oscillation (Grant and Grant, 1989; Grant, 1999). These two factors have allowed us to track changes in populations of uniquely banded and measured finches through time under natural conditions (Grant and Grant, 2002b).

In this paper, I will review the results of a 30-year study investigating the three stages of the speciation cycle carried out by Peter Grant, colleagues and myself on the small island of Daphne Major. I will first briefly describe the island and then discuss lineage divergence and reproductive barriers between species. I will finish with a description of the genetic consequences of a rare founder event that occurred mid-way through our study.

2 Isla Daphne Major

Isla Daphne Major is a small cone of volcanic tuff, approximately 0.75 km. in diameter and 120 m high situated near the center of the archipelago. It is home to four of the fourteen species of Darwin's finches. All four species are in the genus *Geospiza* and are estimated to have arisen from a common ancestor about half a million years ago, according to data in Sato et al. (1999) and Petren et al. (1999). The two most common species are the medium ground finch *Geospiza fortis*, which fluctuates in numbers from over 2 000 individuals to less than 200, and the common cactus finch *G. scandens*, which oscillates between approximately 700 to less than 100 individuals. The small ground finch *G. fuliginosa* is rare, with never more than twelve breeding pairs on the island at any one time. In 1983 we were fortunate to witness a founding event, when the large ground finch *G. magnirostris* established a small breeding colony on the island (Grant et al., 2001). Today this population has grown to almost 50 breeding pairs.

The climate is seasonal, with a hot wet season extending from January to June, and a cool dry season for the rest of the year. Typically, the hot season receives a few strong rainstorms, whereas the cool season is characterized by overcast skies and a sea mist locally known as *garua*. Superimposed on this annual pattern is extreme inter-annual variation in rainfall, ranging from years of heavy rain lasting for 8 months to as many as 32 months of drought when no rain falls and the finches do not breed (Fig.1; Grant and Grant, 1989; Grant, 1999).

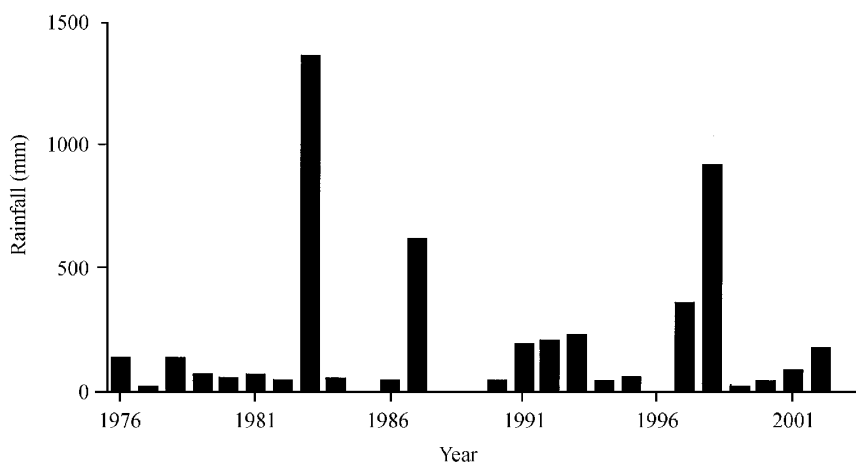


Fig.1 Rainfall on Isla Daphne Major, Galápagos

### 3 Lineage divergence

The study on Daphne Major began in 1973; and in 1977 the first severe drought killed 85% of medium ground finches, including all but one of the offspring hatched in 1976 (Boag and Grant, 1981). The survivors were large-bodied, large-beaked birds capable of foraging on large hard seeds of *Tribulus*, smaller softer seeds having become increasingly rare in the seed bank. Because beak dimensions are highly heritable, offspring born in 1978 had large bodies and beaks. This is predicted from the simple evolutionary equation,  $R = h^2 S$ , where  $h^2$  is the heritability and  $S$  is the selection differential (Boag and Grant, 1981).

*Tribulus* seeds remained abundant in the seed bank, as measured by quadrat data, until 1983 when an El Nino event of unusual length and severity brought unprecedented rain to the islands for a total of eight consecutive months. The rain stimulated immense vegetative growth and reproduction, and completely altered the ecological conditions of the island. *Tribulus* and the cactus *Opuntia*, the producers of hard seeds, were smothered by tall herbs and vines. Of the twenty-four most common plant species growing during that year, twenty-two produce small soft seeds in abundance.

In 1985 a second drought occurred, accompanied by high mortality in the finches. This time, however, small soft seeds made up most of the seed bank. Again selection occurred, this time favoring birds with small pointed beaks capable of picking up small soft seeds (Gibbs and Grant, 1987). From 1985 to 2002 the climate continued to oscillate, with several El Nino years interspersed with droughts of varying magnitude. Measurements of adults and observations of survival before and after the droughts revealed that *G. fortis* and *G. scandens* tracked these

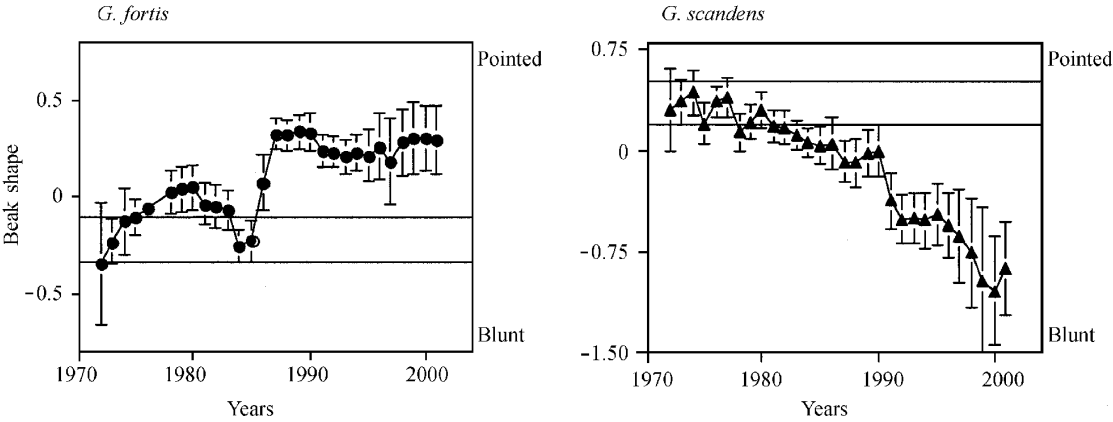
changing ecological conditions through evolutionary responses to each natural selection event. The magnitude of the selection differential at each event depended on the preceding ecological conditions (Grant and Grant, 2002b).

The question then arises: had the mean beak and body size of the population changed as a result of these cumulative selection events over the 30 years of the study? The answer is yes. The cumulative effects of these selection episodes resulted in both populations having a mean body size and beak shape significantly different in 2002 from the means at the beginning of the study in 1973. Shifts in beak shape were particularly pronounced, *G. fortis* having smaller, more pointed beaks and *G. scandens* having smaller, blunter beaks in 2002–2003 than in 1973 (Fig.2; Grant and Grant, 2002b).

These results showed that measurable natural selection events with evolutionary responses occur over short periods of time as a result of climatic and ecological changes. However, they raise two questions. First, how is enough genetic variation maintained in populations of relatively small size to fuel such natural selection episodes? Secondly, if the two species are converging in bill shape, what is the barrier to gene flow between them? The next section describes the nature and strength of the reproductive barrier between these species, and uncovers conditions under which the barrier becomes leaky, where rare hybridization events may lead to introgression.

### 4 Reproductive barrier

*Geospiza fortis* and *G. scandens*, the two most common species on Daphne Major, are not sister taxa but are closely related. They are similar in plumage, males being black, females brown, and they have similar nests and courtship behaviors. They differ in body size, beak morphology and song and hold over-



**Fig.2 Mean beak shape values with 95% confidence intervals across years**  
The beak shape is Principle Component 2 calculated from three beak measurements: beak length, beak depth and beak width. Natural selection and introgression account for the annual changes. The horizontal lines give the confidence intervals around the mean of the 1973 sample, which was the first large sample of the study. Mean beak shape in 2002 lies well outside 1973 confidence limits, the result of *G. fortis* beak shape becoming significantly more pointed and *G. scandens* beak shape becoming significantly blunter in 2002 than it was in 1973. Figure adapted from Grant and Grant (2002a).

lapping territories.

Museum mount and song playback experiments demonstrated that individuals are capable of discriminating between individuals of their own species and other sympatric congeners on the basis of morphology and song (Ratcliffe and Grant, 1983, 1985). Whereas beak and body morphology is highly heritable, song is learned in an imprinting-like fashion. Using playback to young captive birds, Bowman (1961) demonstrated that Darwin's finches learned their song during a short sensitive period early in life, between day 10 and approximately day 30 after hatching. Males sing one simple song, rarely two; and once they have learned it, they keep it unchanged for life. Females do not sing. Most male offspring (~80%) learn their song from their father, the remainder usually from a natal neighbor of the same species (Grant and Grant, 1996a, 1998).

Misimprinting on another species song occurred rarely (~1% of breeding pairs). Observations have shown that this can happen when a pair of *G. scandens* took over a *G. fortis* nest, and jettisoned all but one of the eggs. The *G. fortis* nestling was reared along with its *G. scandens* foster siblings and learned to sing its foster father's song. Other misimprinting events have occurred when the father has died and the young had learnt the song of the nearest natal neighbor, a male of another species, and finally when the nests of two different species were close together and the young of both nests learnt the loudest and most persistent song.

Such misimprinting events can lead to hybridization, as shown by the following results. Of the 392 *G. fortis* females with both father and mate songs recorded, 12 mated with *G. fuliginosa* singing

*G. fortis* songs and hence mated according to song type rather than morphology. *G. fuliginosa* is a 12 gram bird compared to the 18 gram *G. fortis*. Of the 90 *G. scandens* females with the song of both father and mate recorded, four had a *G. scandens* father singing a *G. fortis* song, and all four mated with *G. fortis* males. Once again mating went with song type rather than morphology (Grant and Grant, 1996a, 1998).

A low rate of inter-specific hybridization (approximately 1% of breeding birds) has been relatively constant through the 30 years of our study; but from 1973 to 1983 no F1 hybrid survived long enough to breed. At this time we considered two possible reasons, one genetic (i.e., genetic incompatibility), the other ecological. In the latter case, hybrids with their bills of intermediate size had never been seen to successfully crack *Tribulus* seeds, the predominant (and large, hard) seed in the seed bank in those dry years. They also took significantly longer than *G. scandens* to extract the kernel of *Opuntia* seeds (Grant and Grant, 1996b).

After the switch to a seed bank of predominantly small soft seeds from 1983 on, the hybrids with their intermediate bills were able to feed on small soft seeds and survived long enough to breed. A comparison of the lifetime survival and reproductive success of hybrids with parental species hatched at the same time revealed no genetic incompatibility. This was demonstrated in the three cohorts of 1983, 1987 and 1991 when we had large sample sizes of offspring. In all three, hybrids survived as well as, if not better, than their parental species; and there was no significant difference in number of eggs laid or fledglings reared between hybrids and species (Grant and

Grant, 1998).

The beaks of hybrids are intermediate in size and shape between parental species, but song, being learned, is the same as that of their misimprinted father. Thus a *G. fortis* father misimprinted on *G. scandens* will sing a *G. scandens* song and mate with a *G. scandens* female to produce hybrid male offspring singing a *G. scandens* song or female offspring responsive to the *G. scandens* song. Thus such hybrid males and females backcross to *G. scandens*. Introgression may occur in both directions, but has been greater into *G. scandens*, a result probably enhanced by the skewed sex ratio in the *G. scandens* population after 1991 (in some years as great as 6:1 in favor of males). Introgression increased the phenotypic and genetic variation on which selection can act (Grant and Grant, 1994). Together with selection, it was responsible for the mean beak shape of the *G. scandens* population becoming significantly blunter by 2002 than its form in 1973 at the start of the study (Grant and Grant, 2002b).

Thus song, a learned and culturally transmitted trait, acts as a barrier to interbreeding. Yet it is a leaky barrier due to rare misimprinting on song, leading to hybridization and introgression if the appropriate ecological conditions are available.

## 5 The founding of a new population

In every year since the study began, individuals of *G. magnirostris* visited the island during the dry season; but all disappeared by the onset of the breeding season. At the beginning of the 1982–1983 El Niño event, however, breeding of the residents began unusually early, and five immigrant *G. magnirostris*, three males and two females, stayed to breed. They bred in a combination of pairs and produced a total of 17 offspring. All died except for two brothers and a sister. Thus the second generation was started with a single female breeding with her two brothers. They produced a number of offspring, some of which bred with sibs and parents; and others bred later with new immigrants that had arrived on the island. The founding five *G. magnirostris* were highly variable at 14 microsatellite loci, and had an unusually high heterozygosity index. A comparison over the years showed that although some inbred birds survived extremely well, the mean offspring survival of inbred birds was significantly lower than mean survival in the offspring of outbred birds born in the same year. As expected, the number of alleles in the population dropped over this period of intense inbreeding and then started to rise as new immigrants stayed to breed, each contributing one to three new alleles to the population. In 1991, one exceptionally fit immigrant brought eleven new alleles and a new

song variant to the island. Over the years this bird produced generations of offspring, and his song variant has come to dominate the *G. magnirostris* population on Daphne Major (Grant et al., 2001).

A Pritchard's assignment test applied to data from 14 microsatellite loci revealed that non-breeding immigrants to the island came from four different islands: Marchena, Santiago, Santa Cruz and Isabela. However, the original colonists and all but three of the breeding immigrants came from Santiago. This was unexpected because the nearest island to Daphne is Santa Cruz, only 8 km away, and directly up wind, the prevailing winds being the south-east trade winds; Santiago is further away and downwind. Interestingly, the birds on Santiago are significantly more heterozygous and larger in body size than those from the other three islands (Grant et al., 2001).

For colonization to be successful, theory predicts that the appropriate environmental conditions must be available, the colonists must have sufficient genetic variation to survive the inevitable period of inbreeding, and the initial founding event will be random with respect to genotype. Our data confirms some of these expectations. The *G. magnirostris* founders were unusually variable, and there was an initial loss of heterozygosity due to inbreeding. The unexpected findings were that colonization was not random with respect to island or genotype, and that introgression from new colonists increased genetic variation in the founding population.

## 6 Conclusions

In summary, research on Darwin's finches on Daphne has shown that when environments change, populations track these changes through evolutionary responses to natural selection events, and that an accumulation of these events can lead to significant morphological change in populations over short periods of time. It has also shown that song, a learned and culturally transmitted trait, acts as a barrier to reproduction between species. This barrier can become leaky due to misimprinting on heterotypic song, leading to hybridization and introgression if, but only if, the environment is appropriate for birds of intermediate form to survive. Introgression follows the rule of hybrids backcrossing according to their father's misimprinted song type. An important message for conservation is that neither environments nor species are static entities, and if they are to survive they must be kept in conditions' capable of further change.

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# Resource allocation and life history strategies in birds

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**Abstract** Aspects of resource allocation theory are reviewed. Case history studies of the lesser black-backed gull and red-billed chough are used to illustrate the diverse effects of resource allocation in egg production and related life history strategies on individual development and long-term fitness, with implications for population survival [*Acta Zoologica Sinica* 50 (6): 942—947, 2004].

**Key words** Resource allocation, Life history strategy, Egg production, Chick rearing capacity

## 鸟类的资源分配和生活史策略

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**摘要** 本文综述了对资源分配理论的研究。使用了对小黑背鸥和红嘴山鸦的研究，表明卵产生中的资源分配和相关的的生活史策略对个体发育和长期适合度有多方面的影响，对于种群存活有重要意义 [*动物学报* 50 (6): 942—947, 2004]。

**关键词** 资源分配 生活史策略 卵的产生 育雏能力

### 1 Introduction

The life history strategy of an organism is expressed essentially in its pattern of investment in growth, reproduction and self maintenance. Life history theory attempts to explain the great diversity that we see among species in traits such as size, life span and the pattern of offspring production (Roff, 1992; Stearns, 1992). Life history theory is also concerned with variation in investment in different components of the life cycle within species, and the differing fitness consequences of these investment patterns. The study of resource allocation and life history strategies is obviously a huge topic. In this paper, in addition to confining myself to birds, I shall also focus on intra-specific variation in resources allocated to egg production. The effects of investment patterns in this early stage of reproduction have profound consequences for both parent and offspring, and indeed can span several generations (Lindstrom, 1999; Lumma and Clutton-Brock, 2002; Metcalfe and Monaghan 2001). I shall first outline some relevant concepts from life history theory, and then summarize work that we have been doing on the consequences of variation in investment in egg production for parents and

offspring.

Three basic life history concepts are important in this context; resources are finite; individuals differ in the resources they have available; individuals are mortal.

That resources are finite means that individuals need to optimize their allocation to the differing, and potentially competing, demands made upon them. Thus we should expect trade-offs in resource allocation (Fig.1). However, the negative relationships shown in Fig.1 can be difficult to demonstrate in practice because individuals differ in both the amount of resources at their disposal and in their optimal pattern of resource allocation. We may find, for example, that when we compare individuals of the same species, individuals able to allocate a lot of energy to activity or trait 'A' can also allocate a lot to trait 'B'. This does not mean that there is no competition for resources between traits 'A' and 'B', but may simply reflect the fact that particular individuals are relatively rich with respect to the resource in question. Therefore, experimental manipulation is often needed to demonstrate that the changing of an individual's energy allocation to trait 'A' can have a negative effect on its capacity to invest in trait 'B'.

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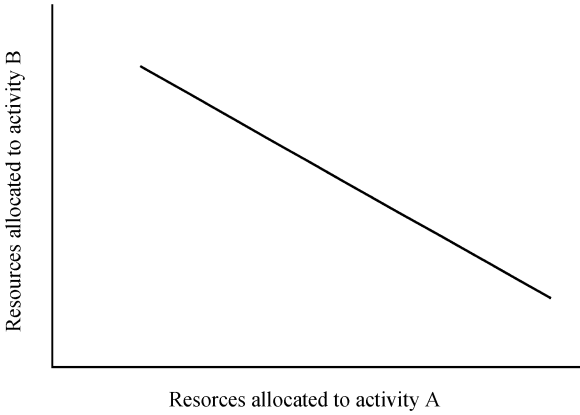


Fig.1 The negative relationship expected in resource allocation when two traits or activities, ‘A’ and ‘B’, compete for the same limiting resources

Mortality factors can be divided into basic types. On the one hand, there are extrinsic causes, such as pathogens, predators and parasites. On the other, there are intrinsic causes, essentially the damaging effects of life itself caused by factors such as free radicals generated during normal metabolic processes; some of this damage can be repaired, and thus the time taken to wear out will vary in relation to the efficacy and deployment of repair mechanisms. That individuals are mortal means that they need to balance their investment patterns in relation to survival prospects—it is not worth investing lots of resources in self maintenance at the expense of reproductive events if the chances are high that you will be eaten by a predator during the coming winter. Considering all of these factors together, we should expect individuals to have different optimal investment patterns, and that these investment patterns may change across an individual’s lifetime.

Birds are particularly interesting in the context of investment in the early stages of life because investment in the egg production stage is high. In comparison with other organisms, birds produce large, yolk-rich eggs. The egg represents a ‘capital’ investment because, apart from heat transfer, the chick receives no further ‘income’ from its mother to fuel its development until after hatching. Receiving all resources in one bundle in the egg contrasts with eutherian mammals, in which developing offspring receive continual income across the placenta. Most other types of organisms have life cycles in which the body architecture is reformed following a larval stage during which further resources are garnered for the adult form. In birds, no such metamorphosis occurs; all of the chick’s development takes place in the egg in precocial birds, and, even in altricial birds, most of the body architecture is formed by the time of hatching. Yet, egg production has often been assumed to be the

‘cheap’ phase in avian reproduction, measured simply in terms of the egg composition, with no account taken of the time to obtain and synthesise key resources and supporting systems, or of the effects on other factors such as flight performance (Monaghan and Nager, 1997). In this paper I will address three main questions that we have been investigating in recent years:

Are there trade-offs between investment in egg production and in other traits?

Are differences in egg production strategies linked to differences in the state of individuals?

Does investment in egg production change across an individual’s lifetime?

2 Are there trade-offs between investment in egg production and other traits?

Clutch size theory has its origins in ornithology, and draws on the pioneering and penetrating insights of David Lack. However, Lack focused very much on the chick rearing phase of avian reproduction, taking the view that ‘clutch size has evolved to correspond with the brood size from which, on average, most young survive, the limit normally being set by the amount of food which the parents can collect for their brood’ (Lack, 1968). Although Lack did qualify this in relation to the varying demands of egg production, his focus on the chick rearing stage has dominated thinking and experimental work relating to the costs of reproduction in birds. Of 105 experimental tests of optimal clutch size in birds up to 1987, 80% of studies manipulated brood size after hatching, thus ignoring costs incurred at earlier stages (Monaghan and Nager, 1997).

That birds were able to rear extra chicks successfully in 75% of such studies led to modifications of Lack’s theory to involve maximization of lifetime fitness rather than the output from a single reproductive event; rearing more chicks today can reduce chick rearing capacity in the future. A further important consideration, however, is the omission of egg production and incubation demands associated with a larger clutch size. In some birds, removal of eggs within 12 hours of their being laid results in prompt replacement; so increased egg production can be stimulated experimentally. And by returning the removed eggs to the nest, clutch size can be enlarged experimentally (Fig.2). When we included these additional costs in common terns *Sterna hirundo*, the capacity to rear enlarged broods disappeared (Fig.3; Heaney and Monaghan, 1995); similar results have since been obtained in other species.

The effect of increased egg production on capacity to rear chicks may come about through negative effects on egg quality or through effects on the

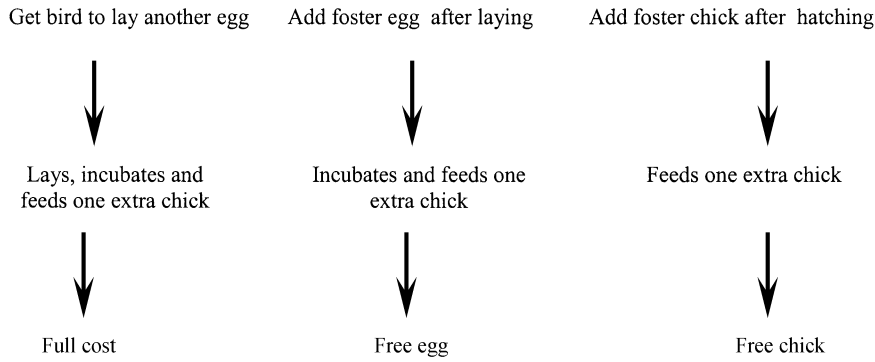


Fig.2 The protocol used for increasing egg production experimentally in species such as common terns that respond to egg removal

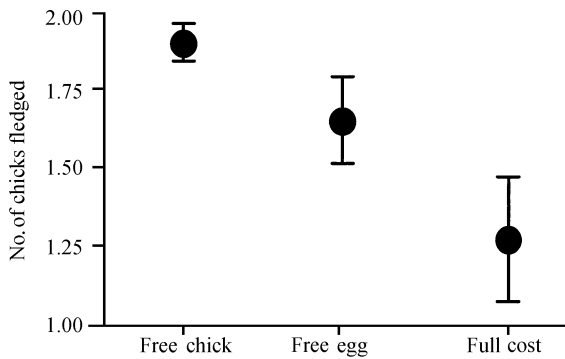


Fig.3 The results of increased egg production as outlined in Fig.2 in the common tern

parents themselves. In a series of experiments on lesser black-backed gulls *Larus fuscus*, which, like the common tern, responds to egg removal by laying more eggs, we have shown that both routes apply. Egg quality can be assessed directly by fostering the 'extra' eggs to other pairs which have not suffered increased egg production costs and then examining the capacity of the fostered eggs to give rise to chicks. The 'parental route' can be examined by stimulating increased egg investment and then giving the pair a foster clutch that has been produced under normal circumstances, thereby removing any egg quality effects. Female condition is reduced even when only one extra egg is laid, and the capacity of a parental pair to rear a fostered three egg clutch is reduced (Monaghan et al., 1998). Furthermore, the nutrient content of the 'extra' eggs is reduced, together with the likelihood of their giving rise to fledged chicks (Monaghan et al., 1995; Nager et al., 2000a).

Interestingly, it is the male chicks that suffer most when egg investment is increased; females in poor condition are less able to rear male chicks, and, independently of maternal condition, male chicks hatching from poor quality eggs are less likely to survive (Nager et al., 1999, 2000b). Overall, this ex-

perimental work shows clearly that when investment in egg production is increased, the capacity to produce high quality eggs and the capacity to rear chicks is reduced. Under natural conditions, of course, both these effects would operate together, because those pairs producing extra eggs are also the ones that rear their hatchlings. We have also found that females whose egg production demands were increased showed lower site return rates, suggesting that trade-offs with survival may also operate (Nager et al., 2001).

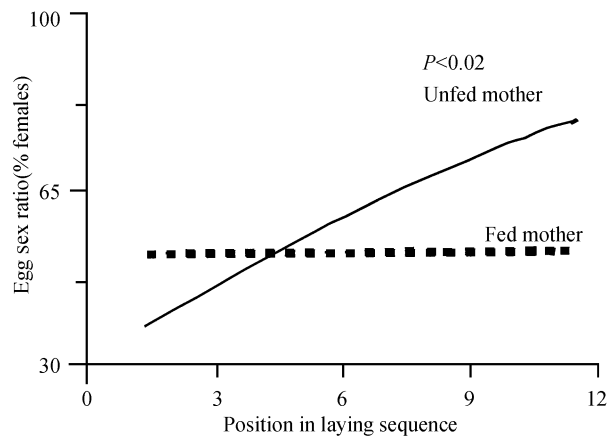
3 Are differences in egg production strategies linked to differences in the state of individuals?

We have tackled this question in a number of ways, including experimental manipulation of maternal condition both upwards and downwards. Reduction of maternal condition was achieved through increased egg production, and enhancement by the provision of supplementary food. One consequence of each in the lesser black-backed gull is summarized here.

As mentioned above, male offspring are adversely affected by increased egg production costs both through the direct effect of poor egg quality and through impairment of the capacity of their parents to rear them. This presumably reflects their higher growth demands. Females in poor condition could therefore be expected to avoid producing male eggs if they possibly can. In fact, this is just what we have observed (Fig.4). Females whose condition has been reduced by increased egg production bias their egg production towards female offspring. That this effect disappears when female condition is maintained during egg laying by provision of supplementary food demonstrates that this is linked to maternal state (Fig.4). Thus females can alter their egg production strategy, in this case the egg sex ratio, in response to their own state during the period of laying.

Other components of the eggs, particularly their





**Fig.4** Changes in the sex ratio of eggs as maternal condition is decreased by continuous egg removal (solid line) The sex ratio becomes progressively more female biased. This effect is removed if maternal condition is maintained by the provision of supplementary food (dotted line).

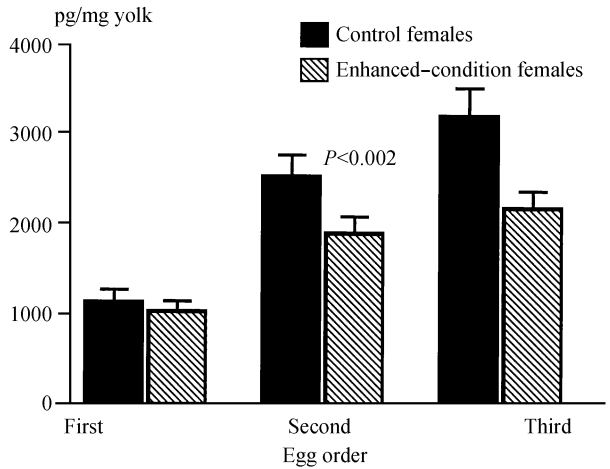
composition, may also be linked to maternal state. There has been considerable interest in the extent to which females can strategically alter the androgen content of their eggs to enhance offspring performance. For species asymmetric in size and with asynchronic hatching such as gulls, it has been suggested that females could improve the survival prospects of last-hatched chicks by increasing egg androgen content, thereby improving the competitive ability of those chicks. This, it is predicted, should happen when maternal condition is good and the prospects of rearing the last chick better. We enhanced maternal condition by the provision of supplementary food prior to and during laying, and examined the androgen content of the eggs (Verboven et al., 2003). The experimental females had higher circulating levels of testosterone at the end of laying than the controls (Fig.5). However, contrary to the predictions, enhanced-condition females laid eggs with less rather than more androgens (Fig.5). These results indicate that egg androgen levels are not a direct reflection of the levels circulating in parental females, and thus that females have some control over egg contents.

Further, they suggest that high androgen levels in eggs may have costs for chicks, such as negative effects of fast growth or impaired immune function. The initial predictions may have been too simplistic, not taking sufficient account of such negative effects. These results also serve to highlight the fact that in carrying out such phenotypic manipulations, we do not always know exactly what components of the phenotype have been altered; changing maternal condition may have a multitude of effects. Maternal state clearly does influence egg production strategies. However, our results also illustrate how important it is to link an understanding of mechanisms with life histo-

ry, because we need a good understanding of the constraints under which strategic allocations of resources operate.

4 Does investment in egg production change across an individual's lifetime?

How investment priorities change with age is a particularly interesting issue, and may involve a complex interplay between constraints and strategy. Fig.6 shows how investment in egg production might be expected to alter with age if individuals are constrained in their performance when young and in old age. When young and old, individuals may be less able to obtain resources than in middle age. Fig.7 shows how strategic investment might change with age. In this case, it is the optimal investment strategy that changes rather than an individual's capacity to acquire resources. Rather than any inability to invest more when young, individuals may choose to invest less in eggs at this stage because of other priorities or effects on subsequent performance.



**Fig.5** Changes in the level of androgens in eggs of the lesser black-backed gull when maternal condition during laying is enhanced experimentally Enhanced-condition females have less androgens in their eggs.

For old birds, it may pay to invest more in egg production instead, at the expense of self maintenance because mortality risks are higher; or it may pay to invest more in self maintenance to prolong life. It will depend very much on the pattern of fitness returns on the investment. Obviously, a mix of shifting optima and constraint will operate, the most likely overall scenario being that individuals hold back when young and are less able to perform well when old. In practice, of course, it is extremely difficult to distinguish between constraint and strategy.

We have been carrying out a study on changes in investment patterns with age in the red-billed cough *Phyrrocorax pyrrhocorax* in Scotland (Reid et al.,

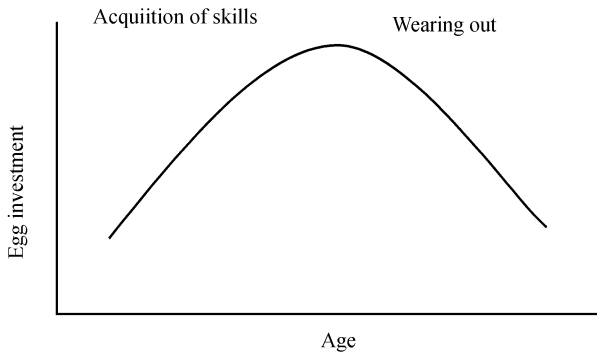


Fig.6 The way in which investment in egg production should change with age if birds are constrained in their capacity to acquire resources when young and in old age

2003a). The change in clutch size with age in this population, corrected for year-by-year seasonal effects, shows the typical dome-shaped relationship found in a number of birds, strongly suggestive of the effects of senescence. However, such cross-sectional data needs to be interpreted with great care. A change in the phenotypic composition of the population is an alternative possibility, in which poor quality individuals are dying young and those laying relatively low clutch sizes are living longest. It would give the same dome-shaped relationship between clutch size and age at the population level.

In choughs, this does occur to some extent; some individuals that start out producing very small clutches also die young, presumably being poor quality individuals. However, those individuals that live to old age also seem to lay relatively small clutches then (Reid et al., 2003b). Thus the decline in mean clutch size in old age classes may not be a consequence of senescence, but rather reflect the differential outcomes of a trade-off between reproductive effort and lifespan. It is important that changes within individuals are also examined. The available data on choughs suggest that

individual performance does decline to some extent (Reid et al., 2003a), and thus the overall pattern at the population level is a combination of senescence and of early mortality in different phenotypes.

## 5 Long term effects of egg investment for offspring

As mentioned earlier in this paper, the conditions experienced by animals during early development may have profound life history consequences. For birds, egg quality and, in altricial birds, the early post-hatching period, are likely to be particularly important. The effects of these early-life factors may not become apparent for some years. Long term effects from early developmental conditions have been reported in a number of species (Lindstrom, 1999; Metcalfe and Monaghan, 2001; Lumma and Clutton-Brock, 2002). Thus, in addition to its immediate effects on offspring development, the pattern of maternal investment in eggs can have important long term consequences for the offspring. Such effects may impact on whole cohorts when environmental conditions are poor. In choughs, for example, the environment experienced by the mother has long term consequences for the breeding life of the offspring (Reid et al., 2003a). In experimental studies on zebra finches *Taeniopygia guttata*, we have shown that nutrition very early in life, though having no detectable effects on external morphology or survival to breeding age, has long term effects on the capacity to assimilate antioxidants, important components in anti-aging defences (Blount et al., 2003). The importance of these long term effects, and their consequences for population dynamics, are only now being appreciated.

## 6 Conclusions

A number of general conclusions can be drawn from our studies, the main points of which are:

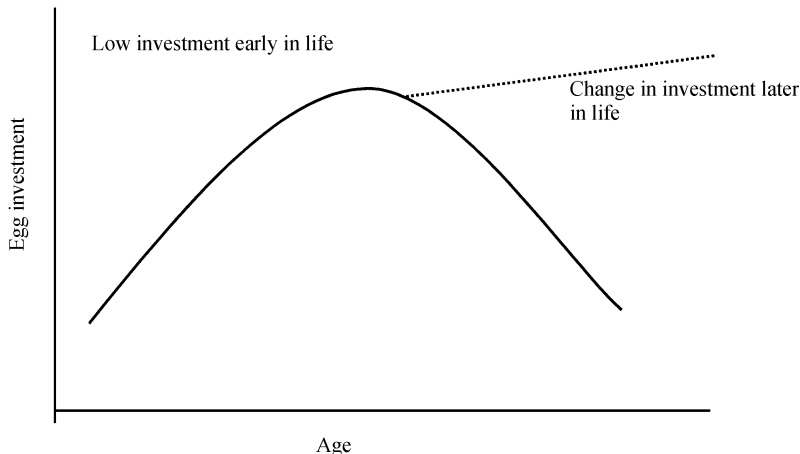


Fig.7 The way in which birds might alter their investment in egg production if the optimal investment pattern changes with age

1) It is now clear from several studies that the costs of egg production in birds are not trivial, and need to be taken into account in assessments of optimal clutch size.

2) The resources allocated to egg production can have profound consequences for parent and offspring fitness over varying time scales.

3) A better understanding is needed of the consequences of long term effects from early-life conditions for individuals and for populations, and of the time scale over which trade-offs operate.

4) It is very difficult to distinguish between strategic investment and constraint, and this needs to be borne in mind in the interpretation of empirical results.

5) A better understanding of what is exactly being changed in phenotypic manipulation experiments is needed.

Studies of proximate mechanisms are crucially important in identifying costs and benefits of different investment patterns and in identifying constraints. Furthermore, studies of investment mechanisms may help us identify the processes that underpin the typically long life-span of birds.

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## Arctic spring: the arrival biology of migrant birds \*

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**Abstract** On arrival in the Arctic, migrant birds must adjust their physiology and behavior to unpredictable snow cover, weather, food sources and predator pressure. In other words they must be resistant to environmental perturbations (stress) so that they can migrate to their tundra nesting areas and settle on territories as soon as possible. They can then begin breeding as soon as when environmental conditions become favorable. They do this partly by using micro-habitats such as areas where snow depth is low, and patches of tundra that melt out rapidly (especially near willows *Salix* sp). Ground temperatures increase dramatically within hours after exposure to sun; and invertebrate activity begins simultaneously. Wind speeds are attenuated almost completely within 10 cm of the ground in willows and tussock tundra. The combination of these conditions provides an ideal refuge, especially for passerine migrants in early spring. However, if conditions worsen, the birds can leave. There are adjustments of the adrenocortical responses to stress because arctic conditions in spring are potentially severe, at least compared with wintering grounds to the south. Secretion of corticosterone in response to acute stress is enhanced at arrival in males, accompanied by a decrease in sensitivity to negative feedback and a change in responsiveness of the adrenal cortex cells to adrenocorticotropin. There is also an increase in levels of corticosterone-binding globulin (CBG) so that the actions of corticosterone are buffered according to the severity of environmental conditions. Regulation at the level of genomic receptors, particularly the low affinity glucocorticosteroid-like receptor for corticosterone in brain and liver, may be important; and non-genomic actions of corticosterone may play a major role too. In other words, the hormone-behavior system associated with arrival biology is highly flexible [*Acta Zoologica Sinica* 50 (6): 948–960, 2004].

**Key words** Arctic, Migration, Stress, Adrenal, Corticosterone, Receptor

## 北极的春季：迁徙鸟类抵达的生物学 \*

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**摘要** 一旦鸟类抵达北极区, 迁徙鸟类必须调整其生理和行为以适应不可预知的雪盖、天气、食物资源和天敌胁迫。换言之, 他们必须抵抗环境干扰(压力)以便尽早迁徙到苔原上的巢区并建立领域。然后, 一旦外界环境有利时, 它们就立即开始繁殖。这些鸟类的繁殖有一部分是利用低雪盖区域的微生境以及雪融较快的苔原斑块(特别是在柳树 *Salix* sp. 附近)。在北极地区, 地面温度在日照若干小时后急剧上升, 同时无脊椎动物开始活动。风速在地面柳枝和生草丛苔原 10 cm 下几乎减弱为零。这些条件结合在一起提供了理想的避难所, 对于早春迁徙到此的雀形目鸟类尤其如此。然而, 如果环境调节变得更为恶劣, 这些鸟类会离开。因为与南方越冬地相比, 春季北极区条件具有潜在的严酷性, 所以鸟类对于应激时的肾上腺皮质反应有所调整。雄鸟到达北极地区时对于剧烈应激刺激下的肾上腺酮的分泌有所提高, 并且伴随着对于负反馈敏感性的下降和肾上腺皮质层细胞对于促肾上腺皮质激素作用反应的变化。同时, 肾上腺酮结合蛋白(CBG)的水平也有所提高, 以至于肾上腺酮的作用在恶劣的环境条件下得到缓冲。基因组受体水平的调节, 尤其是在脑和肝脏中糖皮质激素类固醇类似受体与肾上腺酮的低亲和力, 以及肾上腺酮的非基因组水平的作用, 可能是很重要的。换言之, 与抵达生物学有关的激素-行为系统是高度可变的[*动物学报* 50 (6): 948-960, 2004]。

**关键词** 北极 迁徙 应激 肾上腺 肾上腺酮 感受器

# 1 Introduction

The vagaries of arctic weather in spring have been appreciated by indigenous peoples for millennia. For example, an old Finnish proverb states, “The northern summer is short and variable”. Another proverb from the Saami Reindeer People asserts that “(arctic) spring is the weather’s struggle-time” (Järvinen, 1989). That phrase describes spring in the Arctic perfectly. Weather swings dramatically between winter-like conditions with high winds, low temperatures and snow to sudden breaks in the weather with sunshine and rapidly increasing temperatures. Spring on the North Slope Borough of Alaska is notoriously unpredictable. Temperatures early in spring are more unpredictable than those later in summer (Myers and Pitelka, 1979). At our field site near Toolik Lake (67°N), snow may melt from the tundra as early as the first week in May, but subsequent storms (and temperatures down to -11 °C or lower) may inundate early migrants. In some years, snow and sub-freezing temperatures may persist into late May (Hahn et al., 1995). In the higher Arctic, weather is even more severe.

Virtually all avian species that breed on the arctic tundra are migratory, spending the winter in temperate and tropical latitudes (Piersma, 1994; Pielou, 1994). As a result, arctic weather in spring may present a considerable challenge. On their return in spring, arctic migrants face two major environmental constraints associated with arrival. First, they must establish a breeding territory, attract a mate, and begin nesting on the tundra breeding grounds as early as feasible (O’Reilly and Wingfield, 1995). The ephemeral arctic summer is so brief that birds arriving late may fail to reproduce. Secondly, early arrival in the Arctic is fraught with problems due to capricious

weather. Therefore, birds must also adjust their physiology and behavior to withstand severe weather and sudden food shortages (O’Reilly and Wingfield, 1995). Collectively, these events and the adaptations to deal with them, can be called “arrival biology”. These phenomena have been less well investigated than the “stop-over” biology of migrating birds (Berthold, 1996), but nonetheless may be critical for the transition between vernal migration and onset of breeding.

In this overview we will consider the problems that migrants face, how they move into arctic habitats when conditions are severe, and how they then establish territories in the face of potentially stressful conditions. What are the environmental conditions like in the microhabitats that migrant birds utilize as they move out on to the tundra? These issues are critical if breeding is to begin as soon as possible when the arctic summer begins. Then we will address possible hormone-behavior adaptations and resistance to the potential stress of an arctic spring. Exposure to severe weather in the arctic spring has the potential to induce hormonal responses to stress that in turn have well-known inhibitory effects on reproductive function (e.g., Moore and Miller, 1984; Greenberg and Wingfield, 1987). For example, on May 16 and 17, 2001, night air temperature at Toolik Field Station dropped to -20 °C and did not rise above freezing during the day. Furthermore, blizzards and sub-freezing temperatures can occur unpredictably at any time during the summer, posing further problems for both adults and their young (Astheimer et al., 1992).

Hormone-behavior interactions that allow territory establishment and pair formation to occur in the face of potentially extreme conditions would be adaptive, given that conditions in the immediate future are

likely to be conducive to raising young. Although the physiological ecology of arctic animals in relation to cold has received considerable attention (e.g., Barnes and Deviche, 1995), adaptations of reproductive behavior, their interrelationships with hormones and resistance to environmental stress are just beginning to be explored. Indeed, migrant birds in the Arctic do not have time to be distracted by stress. Do they then modify the adrenocortical hormone response to stress? That is, do they become more resistant? This may be costly in terms of energy, but the benefit is reproductive success.

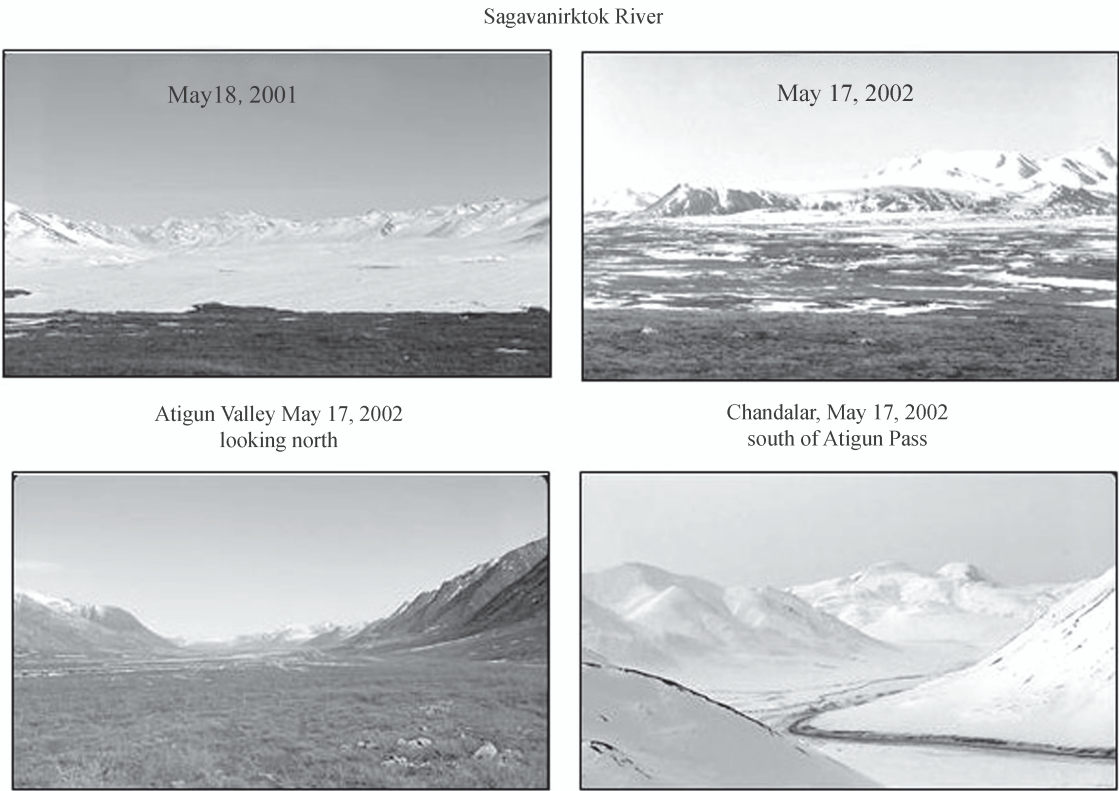
## 2 Arrival biology of migrant birds

Arrival dates of migrant birds at Toolik Lake, Alaska, are precise: May 17 – 22 for both passerines and charadriiforms. Occasionally some individuals may arrive earlier and many arrive much later, but the main influx of migrant birds is generally within these dates. Although the arrival dates of many migrants are consistent from year to year, arctic weather and snow cover can vary dramatically. Snow cover can be complete at arrival time in one year, and very patchy in another (Fig.1). Additionally, year-to-

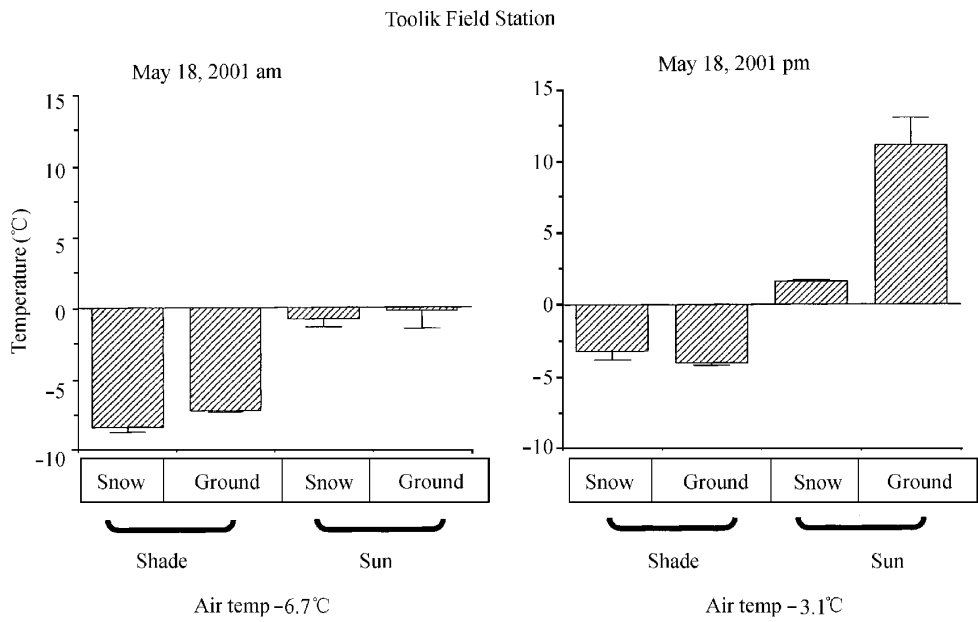
year snow cover along the migratory route may have no bearing on concurrent conditions on the breeding grounds further north (Fig.1). In 2002, snow cover to the south of the Brooks Range in Alaska was complete and very deep at the time passerine migrants were passing through; yet just to the north of Atigun Pass, snow had completely melted. Clearly, migrant birds cannot predict snow cover and depth on the breeding grounds until they arrive. Even after arrival, snow storms with high winds can occur at any time, emphasizing the need for birds to seek out micro-habitats that allow them to shelter from such severe conditions.

### 2.1 Tundra micro-habitats as refuges for migrant passerines

By the third week in May, day length is virtually 24 hours and clearing skies may result in sunshine throughout most of the time. Direct sunlight can penetrate snow at depths up to 20 – 30 cm (depending upon density) and melt the snow pack from the ground up as well as the top down. Thus, depth of snow cover is important in determining which areas tundra will open up first and thus where many migrant birds will settle (Hahn et al., 1995). Wind



**Fig.1 Variation in arctic snow cover among years, and among localities within years**  
The top two panels show how the same area near the Sagavanirktok River, approximately 25 km northeast of Toolik Field Station, North Slope Borough, Alaska, may have different snow cover in different years. The bottom two panels show snow cover north and south of Atigun Pass in the Brooks Range of Alaska. The Dalton Highway crosses the range through that Pass, which is used by large numbers of migrant passerines. It is about 50 km south of Toolik Field Station. Note that on May 17, 2002, snow cover to the south was deep and virtually 100% whereas to the north the tundra was completely exposed.



**Fig. 2** Temperatures recorded at the surface of snow cover and on melted-out tundra in sun and shade  
Temperature probes were placed 1 cm below surfaces to avoid effects of direct sunlight. Temperature recordings were made at 20 locations in snow and on the ground in sun and shade. Cross-hatched bars represent means  $\pm$  standard errors. Air temperatures were recorded at each site, in shade at 1 meter above the surface of snow or ground.

action may scour ridges and some valleys reducing snow cover to a few centimeters. These areas typically melt out very quickly, often within hours. On May 17, 2001, morning snow cover in the Atigun Valley south of Toolik Field Station was over 80%. The day was sunny but windy with air temperatures ranging from  $-20^{\circ}\text{C}$  to  $-3^{\circ}\text{C}$ . Nonetheless, solar energy heated the ground sufficiently to reduce snow cover to about 10% of the valley floor by afternoon. The darker surface of the tundra absorbs radiant energy from the sun, resulting in higher temperatures at ground level compared with open-air temperature, an effect greatly enhanced in sunlight (Fig. 2). Temperatures at ground level in the sun, or just below it in leaf litter at approximately 1 cm depth, can be astonishingly high (Fig. 3).

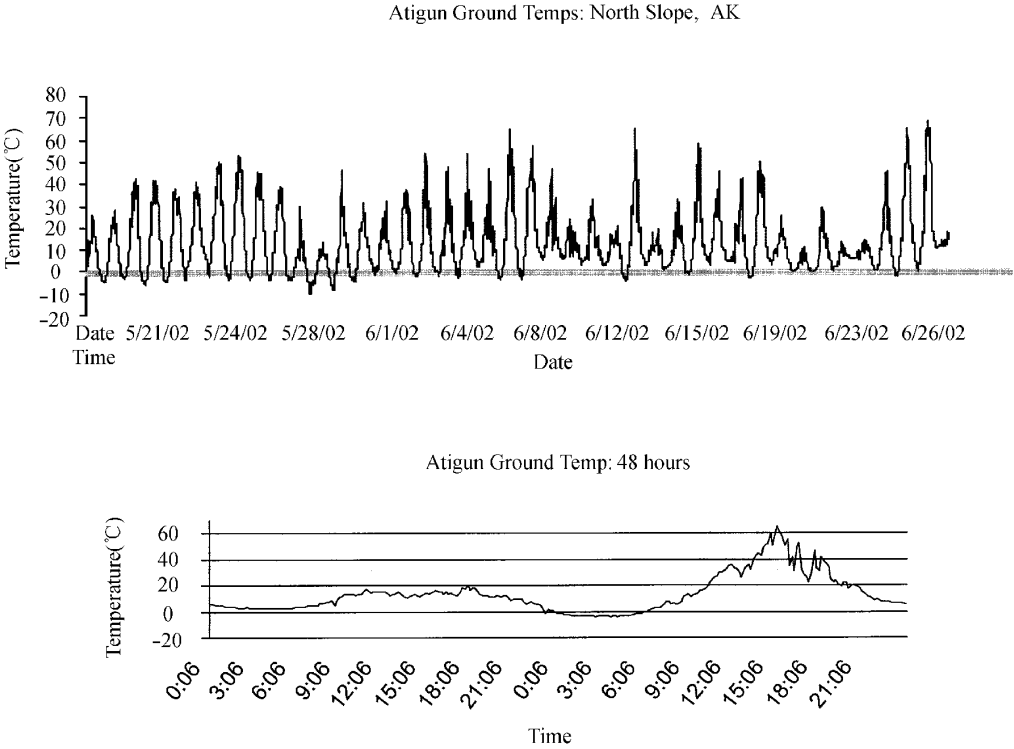
But whenever incident radiation is reduced by cloud, physical barriers (i.e., sun passing behind a mountain), or a low sun angle (e.g., late in the day), temperatures plummet, often to below freezing (Fig. 3). Thus daily cycles of temperature at ground level can fluctuate widely and variably. Patches of tundra can become snow-free extremely rapidly to provide microhabitat for migrant birds. Furthermore, when late spring snow storms occur, the accumulation of snow on these bare patches is much lower than on existing snow pack, suggesting that once microhabitats open up, they can persist even during late snow storms (Hahn et al., 1995).

**2.2 Food sources for migrant birds in the Arctic**

Complete snow cover in spring can cover virtual-

ly all food sources for migrating birds. Both the rock ptarmigan *Lagopus mutus* and willow ptarmigan *L. lagopus* can survive by eating only the tips of willow branches and their buds protruding from snow. Passerines such as snow buntings *Plectrophenax nivalis*, lapland longspurs *Calcarius lapponicus*, and redpolls *Carduelis flammea* can feed on seeds on exposed patches of tundra scoured free of snow by winds. However, they are also exposed to wind chill and possible predation. As soon as tundra patches melt out, increases in ground temperature and wind attenuation allow birds to forage in more benign conditions even though these areas are patchy and unpredictable both spatially and temporally. Such patches always offer seeds from herbs, grasses and shrubs. In some years, masting of the dwarf birch (*Betula* sp.) can result in a super abundance of seeds although this, again, is highly variable both spatially and temporally. As soon as patches of tundra melt out, berries (especially from *Vaccinium* sp.) from the previous summer become uncovered and are eaten in large quantities by migrant passerines. High ground temperatures in melted out areas also result in rapid emergence of arthropods (Insecta and Arachnida). We have observed live dipteran flies, beetles and wolf spiders up to 2 cm long within 2 hours of a patch of tundra becoming snow free. These arthropods are an important source of food for migrant birds.

As the first patches of tundra melt—usually on higher ground where snow depth is less because of wind action—water runs down under the snow pack



**Fig.3** Temperature records using HOBO data loggers at a site in the Atigun Valley about 25 km south of Toolik Field Station during periods of 24 hours of daylight in late May and June

Note that throughout spring into summer there are dramatic fluctuations in ground temperatures. Probes were placed 1 cm beneath leaf litter and other surface vegetation to avoid direct sun light. Temperatures may approach 50°C on sunny days but fall close to freezing on cloudy days. Note also that during the day, ground temperature may vary dramatically according to the angle of sunlight and also if the sun passes behind a mountain ridge, thus shading the ground (lower panel).

to emerge in valleys or shallow depressions. This water may form ephemeral streams and ponds in deeper snow. We have observed migrant passerines and shorebirds (*Scolopacidae*) feeding along the edge of these streams and ponds in snow. Closer inspection revealed that the flow of water under the snow had washed out seeds and arthropods from the surface of the tundra beneath, concentrating them along the edge of the water where the migrant birds had access. These areas are conspicuous because emerging water discolors the snow. Additionally, winter winds form drifts that also act as traps for wind-blown seeds. As the snow melts, water percolating down concentrates seeds usually at the lower edge of the drift; these are thus rich feeding areas for granivorous birds. Additional detritus (dead vegetation and dust) discolors the snow, making such patches conspicuous.

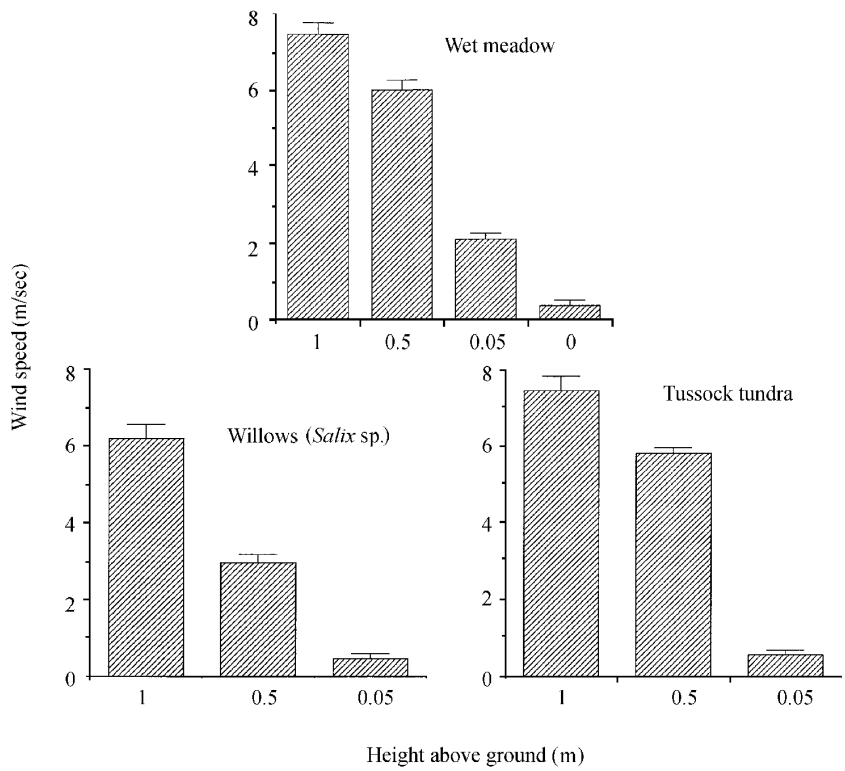
Therefore within hours a frozen, snow covered, landscape can become scattered with patches of open tundra that provide temperatures higher than the surrounding air, shelter from high winds, and multiple sources of food. These resources, however, are still vulnerable to the unpredictable storms that can occur at any time, covering snow-free refuges and refreez-

ing water to lock in washed out food items.

**2.3 Wind attenuation in micro-habitats**

One of the most severe climatic problems for migrant birds on the tundra is high wind speed. This coupled with low temperature can result in extreme wind chill factors. Furthermore, access to foraging patches, and movement between them, can quickly become more restricted; thus competition for food may become a concern in addition to body temperature regulation. Nevertheless, wind speed can be greatly attenuated close to the ground, especially as patches of tundra open up with local snow melt (Fig.4). Even on exposed grassy meadows wind speed is attenuated by about 75% within 5 cm of the ground. In willow patches and tussock tundra, wind speeds may be reduced by over 90% (Fig.4). Thus, the patches of tundra that melt out first are not only much warmer than air temperatures, but they also provide shelter from wind, thereby greatly reducing wind chill. Migrating birds may only be exposed to truly severe conditions when they move from one patch to another over snow-covered areas. However, sudden onset of inclement weather, particularly snow storms, may force them into ever shrinking patches of





**Fig.4 Wind speed attenuation from 1 meter above the ground down to 5 cm in different tundra habitats**  
Cross-hatched bars are means with standard errors ( $n =$  at least 20). Wind speeds were measured with a handheld anemometer.

micro-habitat. This in turn will increase the density of birds in a patch, resulting in competition for food.

**2.4 Habitat use by arriving migrants**

Observations of migrating passerines arriving near their breeding grounds indicate that they use the micro-habitats formed by melting snow. On May 16, 2001, no passerines were to be seen north of the Toolik Field Station, and snow cover was essentially 100%. On May 17, a single horned lark *Eremophila alpestris* and two male lapland longspurs flew by the field station and then disappeared. Further south, toward the Brooks Range, patches of snow began to melt out and passerines were observed moving north from patch to patch (Table 1). At Atigun Pass (1 250 m a.s.l.) snow cover was 100%, but lapland longspurs and American tree sparrows *Spizella arborea*, were flying north through the pass. To the south in the Chandalar Valley, snow cover was much less and water was flowing. Here, flocks of American tree sparrows, American robins *Turdus migratorius*, and Gambel's white-crowned sparrows *Zonotrichia leucophrys gambelii*, were moving north. As the day progressed, flocks of 20 or more lapland longspurs, American tree sparrows and Gambel's white-crowned sparrows crossed the Brooks Range summit near Atigun Pass and descended to the Atigun Valley. One patch of willows (*Salix* sp.) on the north side of Atigun Pass provided the first refuge for passerines crossing the Pass. Passerines were con-

stantly observed flying down from the snow covered pass, and out of a side valley, into the willows. Later in the day, weather conditions deteriorated and over 200 lapland longspurs were observed flying back south toward Atigun Pass. From this first refuge it is only 5 – 8 km to the south side of the pass and the Chandalar valley where conditions were much milder with water flowing. These observations indicate that migrating passerines moving north of the Brooks Range can also return south to more benign conditions over a relatively short distance.

In 2002, conditions at arrival were very different (Fig.1). On May 16, snow cover was less than 25% at Toolik Field Station and water was flowing. Except for 6 redpolls north of the field station, there were no passerines. On the morning of May 17, lapland longspurs began arriving in flocks of 2 – 25; and American tree sparrows and horned larks also appeared further south in the Atigun Valley. South of the Pass, in the Chandalar Valley, snow cover was 100% (Fig.1) and no water was flowing. It was the reverse, climatically, of 2001; but nevertheless, passerines were moving north along the Dalton Highway, the only snow free area by the road. Gambel's white-crowned sparrows were present in the Chandalar Valley but did not appear in the Atigun Valley north of the pass until May 18. Thus, although the first arrivals appeared on the same two days in two years, conditions facing them as they moved north

were very different. Note that in 2002, passerines were generally only found where snow free areas exposed micro-habitats (Table 1).

**Table 1** Observations of arriving migrant birds north of the brooks range in relation to snow cover

Species	Snow	Melt-out Area	Total
Lapland longspur <i>Calcarius lapponicus</i>	1	17	18
American tree sparrow <i>Spizella arborea</i>	1	13	14
White-crowned sparrow <i>Zonotrichia leucophrys gambelii</i>	0	14	14

Numbers of observations of birds in snow-covered areas with no bare ground versus melted-out areas with bare ground, willows (*Salix* sp.), dwarf birch (*Betula* sp.) and tussock tundra. All observations were made when birds were first arriving on May 17 and 18, 2001 and 2002. Right hand column is the total number of observations made. At each observation, snow-covered areas and melt out areas were surveyed. These three species of migrating passerines clearly favored melt-out areas to complete snow cover.

2.5 Predators of migrant birds in the Arctic

There is considerable evidence that populations of predators at northern latitudes can fluctuate dramatically (Newton, 1998). In 2001, at our study site at Toolik Lake, numbers of microtine rodents were very high as were their primary predators: red foxes *Vulpes vulpes*, rough-legged hawks *Buteo lagopus*, short-eared owls *Asio flammeus*, and northern harriers *Circus cyaneus*. As migrant birds began moving on to the tundra, a storm blew in that deposited at least 10 cm of new snow. As a result, the avian predators of voles could presumably no longer locate the rodents and began attacking the flocks of migrant passerines. Additionally, snow cover reduced the number of patches of snow-free micro-habitat, resulting in increased density of migrant birds. Many species formed flocks feeding not only in micro-habitat, but also over snow-covered areas where the seed heads of grasses protruded above the surface. For the next two days, migrants were harassed repeatedly by avian predators that normally did not prey upon them.

Further evidence indicates that predator pressure varies dramatically both within and among years (Newton, 1998). After arrival, nest predation of lapland longspurs fluctuated from year to year (Wingfield and Hunt, 2002). In northern Scandinavia, red fox numbers fluctuated synchronically with vole (*Microtus* sp.) cycles, and foxes switched to ground-nesting birds when voles were scarce. Fox numbers, and their propensity to focus on birds as prey, can thus be unpredictable (Lindstrom et al., 1994). In the islands of northern Sweden, grouse numbers correlated with vole abundance, i. e., predators turned more to grouse when voles were sparse. Removal of predators (red foxes and martens *Martes martes*)

was followed by increased reproductive success in the capercaillie *Tetrao urogallus*, and black grouse *T. tetrix* (Marcström et al., 1988). Clearly, predation can have a major influence on survival during the arrival period, as well as on reproductive success. Moreover, Silverin (1998) showed in the pied flycatcher *Ficedula hypoleuca* that the presence of certain types of nest predator resulted in an increase in corticosterone levels in adults. In the Arctic, the breeding season is so short that birds cannot delay nesting; and if they lose a nest to a predator, re-nesting is rare. Arctic breeding birds simply cannot wait for predator pressure to abate before initiating breeding, unlike the situation in the tropics where the presence of predators may actually be an ultimate factor in regulating the timing of breeding (Morton, 1971).

2.6 Arrival biology: problems facing migrant birds in the Arctic

Although changing day length as spring progresses is a reliable predictor of the short breeding season, migrant birds arriving on the tundra face a number of unpredictable phenomena. They must be flexible to adjust to variable snow cover, and be prepared to respond to further storms. Patchy snow-melt reveals micro-habitats that provide higher temperatures and reduced wind chill while at the same time uncovering variable food resources. However, these habitats can become inaccessible if a severe storm inundates them with snow. Additionally, numbers and types of predators may vary from year to year in an unpredictable manner. These unpredictable characteristics of the Arctic environment require behavioral and physiological plasticity. For example, migrants must be prepared to retreat during storms, at least to the nearest refuge, usually but not always to the south. Responses to these potentially stressful events must achieve a balance between threats posed to survival from physical stress under severe conditions and the risk of missing a single reproductive opportunity. Mechanisms must be in place for responding, or not responding, to potential environmental stressors. Furthermore, these mechanisms must be fine-tuned to a particularly capricious environment. The endocrine mechanisms permitting migrant birds to survive as they arrive on their breeding areas will be considered next.

3 Possible hormonal bases of arrival biology

Arrival on the tundra poses many problems associated with potential stress. Weather is only one source of unpredictable events (labile perturbation factors, LPFs). Other examples include sudden changes in social status (territoriality to flocking as patches of micro-habitat shrink during storms), in-

creased predator numbers, and decreased food resources (Wingfield et al., 1998; Wingfield and Ramenofsky, 1999; Wingfield and Romero, 2000). Environmental cues such as changing day length allow migrants to predict future events and to time migration to arrive in the third week of May. However, responses to LPFs require more rapid facultative changes in behavior and physiology than follow those from anticipation. These responses have been collectively termed the emergency life history stage (ELHS) that diverts the individual into a physiological and behavioral state that will allow survival in the best condition possible (Wingfield et al., 1998). Although the ELHS is highly adaptive in most conditions, it may actually be detrimental in migrants arriving on the tundra because the birds must settle on breeding territories as soon as possible so that breeding can begin as soon as local conditions allow. Thus it was hypothesized that, during arrival, there may be adjustment of hormonal responses to stress that allow individuals some degree of “stress-resistance” until environmental conditions improve (Wingfield, 1994).

Vertebrates activate the hypothalamo-pituitary adrenal (HPA) axis in response to LPFs (Greenberg and Wingfield, 1987). Adrenocorticotropin (ACTH) is released from the precursor molecule pro-opiomelanocortin in the anterior pituitary under the control of corticotropin-releasing hormone (CRH) from the hypothalamus. ACTH acts primarily on the adrenocortical cells to promote synthesis and secretion of glucocorticosteroids. In birds, the primary glucocorticosteroid is corticosterone. Chronic elevation of corticosterone over weeks can have severe debilitating effects, such as inhibition of the reproductive system, suppression of the immune system, promotion of severe protein loss from skeletal muscle, disruption of second cell messengers (particularly the arachidonic acid cascade), neuronal cell death and suppression of growth (e.g., Sapolsky et al., 2000). These effects would be clearly detrimental to an individual at any time. However, effects of transitory increases in corticosterone in response to LPFs are more adaptive. In birds and mammals, corticosterone has several behavioral and physiological effects that promote fitness, at least in the short term. These include suppression of reproductive behavior without inhibiting the reproductive system, regulation of the immune system, increased gluconeogenesis, regulation of foraging behavior, promotion of escape (irruptive) behavior by day, promotion of night restfulness, and facilitation of recovery on return to normal life history stage (Sapolsky et al., 2000; Wingfield and Romero, 2000).

These short-term effects of corticosterone during

responses to LPFs suppress “unnecessary” physiological and behavioral functions, activate alternate behavioral and physiological patterns that promote survival (i.e., temporary emergency behavior) and avoid the long-term, detrimental effects of stress-induced high levels of corticosterone. But, on spring arrival in the Arctic, migrants have to resist the potential for stress when exposed to many LPFs. Our hypothesis is that the adrenocortical response to LPFs is modulated, at least in the short term, to allow migrants to continue to arrive in the face of severe conditions. More specifically, we predict that the stress-induced increase in corticosterone levels would be inhibited at arrival, thus providing resistance to potential stress from severe weather. This may be energetically expensive, especially when spring storms occur. The benefit, however, is enhanced reproductive success.

### 3.1 Modulation of the adrenocortical response to stress

There is extensive evidence that birds can adjust the responsiveness of the HPA axis to the effects of LPFs. To measure responsiveness to stress we take advantage of the fact that capture, handling and restraint of wild birds induces a strong activation of the HPA axis, resulting in a rapid increase in plasma levels of corticosterone within 3 minutes, reaching a maximum by 10–60 minutes. We can collect a small blood sample within 2 minutes. The level of corticosterone in this sample represents the baseline (close to the level just prior to capture). Further small blood samples can then be taken at intervals (e.g. 5, 10, 30 and 60 minutes) to track the increase of corticosterone secretion following the stress of capture, handling and restraint. Examples of this “capture stress” response are given in Fig. 5. It is important to bear in mind that most, if not all, stressors have the potential to elicit increases in corticosterone secretion, although the time, course and extent of the response may be different between reaction to a predator and, for example, a severe weather event (Wingfield, 1994; Wingfield et al., 1995a, b, 1998). The baseline level, the rate of increase of plasma corticosterone levels following capture, and the maximum level attained are measures of the stress response and can be compared across seasons, habitats, ages and genders.

In arctic birds, there is a trend for this responsiveness to decline when birds are breeding (Wingfield, 1994; Wingfield et al., 1995b). Furthermore, this reduced sensitivity to stress appears to be greater in the sex responsible for most parental care (O'Reilly and Wingfield, 2001) and in the most severe environments (Wingfield, 1994). Thus, reduced sensitivity to acute stress when arctic birds are breeding supports our original hypothesis. Moreover, if prolonged severe weather resulted in abandonment of the

nest, then the adrenocortical response to capture stress increased as birds formed flocks roaming the snow-covered tundra (Astheimer et al., 1995). This observation also suggests that responsiveness to stress is suppressed during breeding.

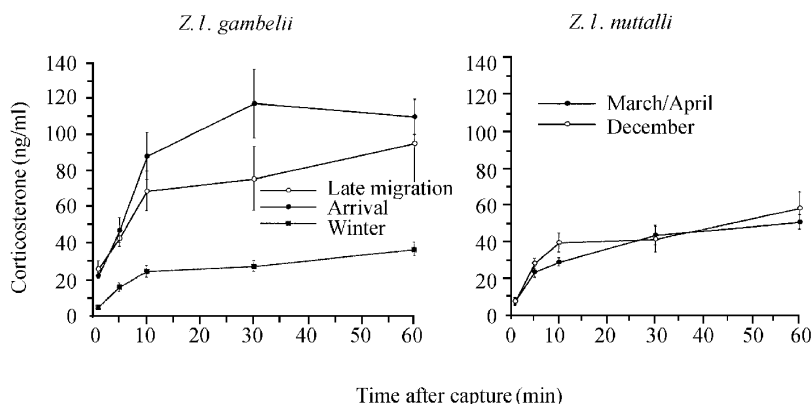
If, however, we now look at the corticosterone response to capture stress in birds arriving on the tundra, we find a different picture. In Gambel's white-crowned sparrow, the response to stress in males actually increased markedly over that recorded in winter, prior to migration (Fig.5, Romero et al., 1997). Eventually, the response to stress would be inhibited as the males progressed into the nesting phase (Holberton and Wingfield, 2003); but on arrival it was greatly enhanced. Note that a non-migratory race of white-crowned sparrow *Z. l. nuttalli*, breeding at mid-latitudes (central coastal California), did not show this type of modulation of the adrenocortical response to stress (Fig.5). Similar enhancement of the response to capture stress at the beginning of the nesting season has now been demonstrated in other avian populations breeding at the northern edge of their range, as in the bush warbler *Cettia di- phone* in Hokkaido, Japan (Wingfield et al., 1995a), the snow bunting and lapland longspur arriving at the northern edge of their range at Thule, Greenland (77°N, J.C. Wingfield et al., unpublished), and arriving red knots *Calidris canutus*, at Alert, Ellesmere Island, Canada (82°N; Reneerkens et al., 2002).

In Gambel's white-crowned sparrow, the increase in adrenocortical sensitivity to stress was accompanied by decreased sensitivity to glucocorticosteroid feedback (Astheimer et al., 1994), and by enhanced sensitivity of adrenal cortex to ACTH

(Romero and Wingfield, 1998), thus producing an overall increase in baseline as well as capture stress induced-plasma levels of corticosterone. This remarkable increase in sensitivity to acute stress contradicts our original hypothesis. However, recent evidence has shown that in birds, as in perhaps most vertebrates, circulating glucocorticosteroids are bound to a protein, corticosteroid-binding globulin (CBG). While bound to this protein, it has been proposed that glucocorticosteroids are largely inactive because they are unable to enter cells and interact with receptors that mediate biological actions (Breuner and Orchinik, 2001, 2002). If this is the case, then it is possible that CBG levels could be modulated, thus buffering such marked increases in responsiveness to LPFs.

#### 4 A corticosterone-binding globulin (CBG) buffer hypothesis

Although the adrenocortical response to acute stress is enhanced at arrival in male Gambel's white-crowned sparrows, there was also an increase in CBG levels that may buffer stress-induced increases in corticosterone; hence the response of free (unbound) corticosterone able to enter cells and interact with receptors was actually reduced (Romero and Wingfield, 1999; Breuner et al., 2003). Thus, although baseline levels of corticosterone, and stress levels after 30 minutes of capture stress, were elevated, high CBG binding capacity of the plasma may actually bind most of this glucocorticosteroid (Fig.5). Indeed, in a comparison of subspecies of the White-crowned Sparrow, it has been shown that the mid-latitude breeding *Z. l. pugetensis* also does not increase responsiveness to stress in early spring, just prior to breeding, and it remains stable throughout the nesting phase



**Fig.5** Effects of capture, handling and restraint on plasma levels of corticosterone in free-living white-crowned sparrows *Zonotrichia leucophrys*

The left hand panel shows seasonal changes in hormone response to capture stress in *Z. l. gambelii*. Note that during migration (in central Alaska), the baseline and maximum plasma levels of corticosterone increase, with a further elevation of maximum levels on arrival on the breeding grounds at Toolik Field Station. In the right hand panel, the hormonal response to capture stress shows no such seasonal change in non-migratory *Z. l. nuttalli* sampled at Bodega Bay, central California.

(J. C. Wingfield, unpublished). Lower binding capacity of CBG measured in *Z. l. pugetensis* sampled later in the season may actually result in higher free levels of corticosterone 30 minutes post-capture than in *Z. l. gambelii* (Breuner et al., 2003). If plasma levels of corticosterone, CBG binding capacity, and affinity for corticosterone are known, then free corticosterone levels in blood can be calculated to give an estimated level of potentially biologically active steroid (Breuner et al., 2003). Such a calculation shows that at least during the nesting phase, and despite higher baseline and 30 minute post-capture stress levels of corticosterone in *Z. l. gambelii* males, the free levels are actually reduced compared to those in samples of male *Z. l. pugetensis* collected at a similar phase (Breuner et al., 2003). These data are consistent with our hypothesis that the adrenocortical response to stress, at least in terms of the free level of hormone generated in response to a LPF, is actually reduced.

There is precedent for this kind of regulation in other avian species. In the house sparrow *Passer domesticus*, seasonal changes in adrenocortical responses to capture stress are buffered by changes in CBG binding capacity of plasma so that the free level of corticosterone 30 minutes post-capture does not change (Breuner and Orchinik, 2001, 2002). So why show seasonal modulation of the adrenocortical response to stress (LPFs) and then buffer the response by modulating CBG binding capacity in blood? It is possible that the buffering action of CBG may maximize flexibility of metabolic and behavioral responses to LPFs at different times of the year. For this to work, CBG levels in blood should be regulated as well, especially for short-term finely-tuned free levels of corticosterone that are then able to enter cells and bind to receptors (Breuner and Orchinik, 2002).

There is recent evidence that CBG binding capacity may be regulated within hours if a LPF persists. In captive male *Z. l. gambelii*, food restriction (to mimic the effects of a storm that covers food resources) increased plasma corticosterone levels for 2 hours but had no effect on CBG binding capacity. After 22 hours of food restriction, corticosterone levels matched those of the controls, but CBG levels had declined significantly, thus increasing free corticosterone titers (Lynn et al., 2003). In this scenario we see a fairly rapid (within 2 hours) response to food restriction, even before major metabolic stress has set in, after which CBG levels declined as the period of food restriction persisted, thus releasing corticosterone to increase the free levels above those of controls.

Clearly, the hormone-behavior system associated with arrival biology is highly flexible, allowing an ap-

parent adrenocortical response to LPFs but buffering the early effects with high initial CBG binding. If a LPF persists, then a decline in CBG releases corticosterone into cells. Although much more work needs to be done to assess how quickly the changes in CBG binding capacity can occur, this may be a very elegant system by which migrant birds arriving on the arctic tundra, or other habitats, may retain the activity of the HPA axis intact, but modulate the expression of the CBG gene (or down-stream translation of that gene) and thus access of hormone by receptors. The next question is: are corticosterone receptors also modulated in migrant birds arriving in the Arctic?

## 5 Corticosteroid receptors in target tissues

Before the question of cellular receptor regulation for corticosterone can be answered, it is necessary to describe the types of receptors present in the tissues of passerine birds. In mammals, there are two genomic receptors: the high affinity, mineralocorticoid (MR) receptor activated at basal (normal) levels, and the low affinity, glucocorticoid (GR) receptor activated at higher "stress" levels. Evidence to date suggests that a similar system operates in passerines (Breuner and Orchinik, 2001; Breuner et al., 2003). *In vitro* binding experiments show that the MR-like receptor in sparrows has high affinity binding for corticosterone (as in mammals) but has different specificity characteristics, suggesting the sparrow receptor might be different from the mammalian one (Breuner et al., 2003). However, the GR-like receptor with a lower binding affinity for corticosterone does appear to be similar in specificity to that of mammals (Breuner and Orchinik, 2001; Breuner et al., 2001, 2003). Both MR-like and GR-like intracellular receptors for corticosterone were found in the brain and liver of house sparrows and three taxa of white-crowned sparrow (Breuner et al., 2003). Because the higher levels of corticosterone in response to LPFs are of primary interest here (they mediate the physiological and behavioral components of the ELHS), we now focus on the GR-like receptor because it is only activated at higher circulating concentrations of corticosterone.

There were no significant differences in the binding capacity of GR-like receptors in either the liver or the brain of *Z. l. gambelii* (arctic-breeding) or of *Z. l. pugetensis* (mid-latitude-breeding) males. Because the plasma level of corticosterone, CBG binding capacity, and MR-like receptor capacity were measured, this provides a general model of corticosterone action, estimating the number of receptors occupied at given free corticosterone levels. Using mean levels of free corticosterone and GR-like receptor capacity, the receptor occupancy during

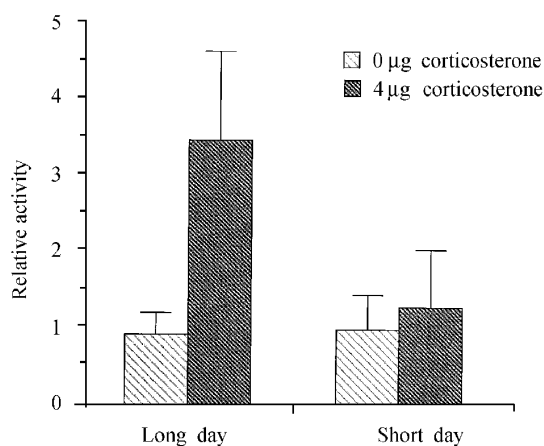
stress can now be calculated. Although the binding capacity of GR-like receptors did not vary between the two taxa of white-crowned sparrow, there did appear to be more GR-like receptors occupied by corticosterone 30 minutes post-capture in both liver and brain of *Z. l. pugetensis* (Breuner et al., 2003). These data strengthen the argument that CBG buffering actually decreases sensitivity to LPFs in arriving *Z. l. gambelii*.

There is also a putative non-genomic receptor mediating more rapid effects of glucocorticosteroids, within minutes (Breuner et al., 1998). Male white-crowned sparrows fed meal worms injected with known doses of corticosterone showed elevated plasma levels of corticosterone within 15 minutes of ingestion. Ingested corticosterone was cleared by 1 hour post-ingestion, thus mimicking a transient LPF that activates the HPA axis. Behavioral observations indicate that this non-invasive way of administering corticosterone results in an increase in perch-hopping activity within about 10 minutes, compared with controls. Such rapid action is not consistent with genomic receptors that require at least 30 minutes and usually several hours to react (Breuner et al., 1998; Breuner and Orchinik, 2002; Orchinik et al., 2002). Interestingly, the lower dose of corticosterone consistent with intermediate plasma levels was effective, but not a higher dose consistent with high stress levels (Breuner et al., 1998). Therefore, it is possible that rapid, non-genomic effects of corticosterone on activity may be important in arriving birds that are not subjected to severe LPFs. Furthermore, the actions of this membrane-type receptor appear to be greatest in spring, when arrival occurs, and less so in winter (Fig. 6, Breuner and Wingfield, 2000), suggesting that such rapid effects on activity may be related specifically to arrival biology and perhaps also the onset of breeding.

## 6 Mechanisms underlying arrival biology of migrant birds in the Arctic

Cumulatively, data suggest that the adrenocortical response to stress is increased on arrival in spring concomitant with reduced sensitivity to glucocorticosteroid feedback and enhanced adrenal sensitivity to ACTH. However, elevated binding capacity of CBG buffers this increase so that free circulating levels of corticosterone are actually reduced. Binding capacity of the GR-like genomic receptors for corticosterone does not appear to differ in the brain or liver tissue of *Z. l. gambelii* compared with *Z. l. pugetensis*. Yet despite higher baseline concentrations of corticosterone in arriving *Z. l. gambelii*, CBG buffering action can cause the numbers of GR-like receptors occupied to actually fall after 30 minutes of post-capture

stress. Additionally, we have shown that levels of CBG (measured as binding capacity in plasma) can also be regulated over 24 hours if an LPF persists. Thus, although the adrenocortical response to stress is elevated in arriving migrants in the Arctic, the effective free level of corticosterone is reduced compared with that in congeners at mid-latitudes. Furthermore, the binding dynamics of both CBG and GR-like receptors in tissues may result in fewer genomic receptors being occupied than originally thought. Counter this with independent regulation of CBG binding and there emerges a highly flexible system fine-tuning an individual's response to an LPF, either towards more resistance (favoring establishment of a territory and onset of breeding) or greater sensitivity (favoring retreat to a refuge and delayed onset of breeding).



**Fig.6 Modulation of non-genomic receptor activity for corticosterone in white-crowned sparrows *Zonotrichia leucophrys gambelii* as indicated by behavioral responses to non-invasive administration of corticosterone**

Only on long days (similar to time of breeding) was corticosterone able to increase activity rapidly. From Breuner and Wingfield (2000).

There may also be adaptations of the hormone-behavior systems that do not involve stress modulation. The rapid acting non-genomic receptor effect on activity appears to be effective at baseline levels of circulating corticosterone, and only in long-day male *Z. l. gambelii*, at a stage equivalent to arrival in the field. The increase in perch-hopping activity may be related to final stages of spring migration in the Arctic when birds arrive on their breeding grounds, locate suitable breeding habitat, and familiarize themselves with immediate food sources should conditions deteriorate and conceal them. Stress levels of corticosterone, as generated by subcutaneous implants of corticosterone in the absence of food, also increase perch-hopping activity as well as escape-type behavior in male *Z. l. gambelii* (Astheimer et al., 1992). This behavior is different from that observed by Bre-

uner et al. (1998), and is perhaps consistent with leaving the area (irruptive migration) sometimes seen in response to severe and prolonged LPFs (Wingfield, 2003). But, how would one hormone, corticosterone, regulate both types of activity? Certainly different receptor types may be involved, but further evidence suggests that irruptive behavior, and its perch hopping equivalent, is also influenced by CRF injected centrally into the third ventricle of male *Z. l. gambelii* in the laboratory (Maney and Wingfield, 1998), as well as by central injections of CRF into the lateral ventricles of male *Z. l. gambelii* in the field (Romero et al., 1998). Thus corticosterone action may play a permissive role for secretion of brain peptides, or other substances, to provide specific behaviors for particular environmental scenarios. Further research will determine whether such interactions occur in the regulation of activity associated with arrival biology.

Although much more research needs to be done, the concept of arrival biology of migrant birds is emerging. Additionally, we have the beginnings of a scheme for the hormonal regulation of the behavior and physiology of this phenomenon. There appears to be a highly flexible control system that allows migrants to respond rapidly and adaptively to a highly unpredictable environment, thus maximizing fitness by allowing them to settle on suitable habitat and begin breeding as soon as possible. Yet more hormone-behavior adaptations may be found, particularly in relation to actions of sex steroids such as testosterone on territorial aggression and pair formation. Obviously, the study of arrival biology of migrant birds involves a highly integrative mix of behavioral, physiological and landscape ecology, and organismal, cell and molecular endocrinology.

## 7 Future directions

Much remains to be revealed in the hormone-behavior interrelationships of and ecological factors associated with arrival biology. Are there additional hormone systems involved, and do different species integrate the physiology and behavior of arrival in similar or different ways? The arrival biology of migrant birds can be studied in other regions on the earth, such as mountains, deserts and mesic habitats. Are similar control mechanisms in place, and do these differ from the well-studied examples of stopover biology during migration in spring and autumn? The arrival biology of migrant birds at their wintering areas in autumn should also be of interest, as it is likely to be rather different from that in spring.

Other intriguing questions include: what are the environmental cues triggering changes in CBG, genomic and membrane receptors associated with arrival

biology? Will global climate change increase environmental unpredictability, making phenotypic flexibility a critical factor in dealing with long-term changes in the environment? Can arctic animals adjust accordingly? Will the highly plastic hormone-behavior interaction system underlying arrival biology enable them to cope? It is hoped that this paper will have heuristic value in characterizing the phenomenon of arrival biology. The possibilities for truly integrative research from molecules to populations are challenging.

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## The costs of immunity

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**Abstract** The costs of development of the immune system come primarily from the expenditure of energy to fuel the inefficient process of developing antigen recognition diversity in B and T lymphocytes and to provide substrates (e.g., amino acids and lipids) for the initial burst of leukopoiesis needed to supply the late embryo and hatchling with leukocytes. The costs of maintaining the immune system are related to allocating nutrients for the continued production of leukocytes, immunoglobulin, and other plasma proteins to replace those lost during normal turnover of cells and extra-cellular proteins. The costs of using the immune system to thwart the invasion of potential pathogens come in two primary forms. First, there are losses in tissue function that result from damage incurred when leukocytes engage their effector mechanisms and damage tissue integrity and host cell viability (collateral damage). Secondly, there are nutritional costs in mobilizing the responding cell types and fueling their effector functions. The primary cost of an authentic pathogen challenge is in the systemic acute phase response, especially recruitment of the liver, to assist the immune system by producing protective proteins [*Acta Zoologica Sinica* 50 (6): 961–969, 2004].

**Key words** Immunity, Innate, Adaptive, Costs, Maintenance, Developmental

## 免疫的代价

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**摘要** 免疫系统发育的代价主要是为 B 淋巴细胞和 T 淋巴细胞发育抗原识别多样性时的低效率过程提供能量, 为开始形成白血球提供基质 (如氨基酸和脂肪), 并为胚胎和雏鸟提供白细胞。维持免疫系统的代价与持续产生白细胞、免疫球蛋白以及其它血浆蛋白时的营养分配有关, 这些血浆蛋白用于取代在正常的细胞代谢中丢失的蛋白质以及细胞间的蛋白质。利用免疫系统阻碍可能的病源体入侵的代价有两种主要形式。第一, 由于白细胞参与效应子机制时发生的损害、组织整合性以及寄主细胞的存活力的损伤, 组织功能有一些损失。第二, 在活化相应类型的细胞并产生其效应子作用时存在着营养耗费。病源体挑战所带来的主要代价是系统的急性期反应 (特别是肝脏的复原) 通过产生保护性的蛋白质来帮助免疫系统 [*动物学报* 50 (6): 961–969, 2004]。

**关键词** 免疫 先天 适应性 代价 维持 发育

## 1 Introduction

Vertebrates shield themselves against virus, bacteria, and eukaryotic parasites by investing in a multilayered and complex system of protection: the immune system. Among birds, there is marked interspecies and intraspecies variation in susceptibility to challenges by pathogens. Given that there are costs attributable to the processes providing protection, it can be expected that much of the variability in pathogen susceptibility is due to differing investments in the size and quality of the immune system. Evidence from genetic selection studies (Siegel et al., 1982b; Parmentier et al., 1995; Parmentier et al.,

1996; Qureshi and Havenstein, 1994; Martin et al., 1990) and from interspecies and intraspecies comparisons (Moller et al., 2003; Martin et al., 2003; Tella et al., 2002) support this contention. Studies in physiological ecology and theoretical immunology often refer to the “costs” in terms of resources, such as the energy needed to mount an immune response, or the trade-offs between immunocompetence and other nutrient-requiring functions (Read and Allen, 2000). An accounting of these costs should be precise for birds, for these theories and arguments to have a sound quantitative basis. However, the costs of immunity have rarely been described with precision, so the importance of trade-offs between immunity and

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other physiological processes remains obscure. Given that investment in self-maintenance, especially immunity, is presumed to be an important constraint in the diversification of life-histories (Ricklefs and Wikelski, 2003; Klasing and Leshchinsky, 1999), a greater appreciation of the costs of immunity is needed.

The immune system has many layers and is pervasive within most physiological processes of the body. All cells have mechanisms that provide self-maintenance and thwart infectious challenges. For example, foreign RNA is silenced by an intricate molecular mechanism that minimizes the ability of viruses to commandeer the translational machinery of a cell (Plasterk, 2002). Though all body cells have defensive pathways, leukocytes are the professional cells of the immune system and are responsible for detection of pathogens, production of molecules to eliminate the pathogen, and alerting nervous, endocrine and other regulatory systems of infectious challenges. Leukocyte functions are typically divided into innate and adaptive components. Innate immunity is mediated predominantly by phagocytes and is crucial for defense against novel pathogens. Adaptive immunity is mediated predominantly by lymphocytes, and requires four or more days of activation before contributing significantly to protection against novel pathogens. Notably, subsequent challenges by a pathogen are quickly and effectively thwarted by adaptive immunity because of its memory capabilities, whereas innate immunity is no more effective against a second challenge than it was against the first.

## 2 Estimating the cost of immunity

As in all physiological processes, the nutritional costs of immunity are best subdivided into three components: those of developing the immune system, those of maintaining that system in working order, and those involved in use of the system to thwart a parasitic invasion. Development of the immune system is defined as the initial differentiation and selection events in the thymus and bursa that generate a diverse pool of lymphocytes expressing thousands of unique pathogen receptors needed to identify potential pathogens. Development also includes the clonal proliferation of all leukocyte populations and their occupation of epithelia and secondary lymphoid organs. The maintenance state is defined as a quiescent immune system engaged in routine functions such as clearing apoptotic cells that result from normal cell turnover. The use of the immune system is defined as a response to a foreign organism or molecule designed to contain or deactivate it.

Use of the immune system includes phagocytosis, the acute phase response, proliferation of antigen-specific lymphocytes, antibody production, and cell-

mediated cytotoxicity. Current theory predicts that there is a tradeoff between inductive versus constitutive types of protection (Shudo and Iwasa, 2002; Schmid-Hempel and Ebert, 2003). Maintaining constitutive levels of protective cells and proteins at protective levels should provide the most rapid and effective defense, but it has high nutritional costs. Alternatively, a low level of constitutive production of protective factors, with rapid induction following a pathogen challenge, is predicted to have cheaper cost if lower protective value. From this viewpoint, constitutive production of leukocytes and protective proteins is a maintenance activity, while the increase due to a challenge is considered use of the system.

The cost of immunity can be estimated directly or indirectly. Direct estimates are derived from population dynamics, energy expenditure, and rates of material accretion by leukocytes and other cells that contribute to immunity. Indirect estimates can be obtained by examining the extent of trade-offs in competing physiological processes that occur due to immune processes. Ultimately, our confidence in the cost of immunity depends on the congruence of direct and indirect estimates.

Quantitative measurements of leukocytes and their products typically require monoclonal antibodies and other reagents that are species-specific and unavailable except for agriculturally important species. For this reason, direct estimates of the cost of immunity in the Aves are available only for chickens *Gallus gallus*. However, indirect estimates are not particularly reagent-dependent and can be obtained across avian orders; though to date, most of the work has also used the Galliformes, especially the chicken and Japanese quail *Coturnix coturnix japonica*.

### 2.1 Direct estimates

The nutritional costs of many physiological processes have been well defined. For example, the resting metabolic rate of many hundreds of avian species has been measured and often re-measured. The additional costs to support activity, thermoregulation, growth, molt, and egg production have likewise been detailed with precision. Data on the rate of tissue accretion, the nutrient composition of tissues, and the rates of macromolecule turnover have provided a firm scientific basis for estimating the nutritional demands of growth, molting, and egg production (Klasing, 1998b; National Research Council, 1994). Unfortunately, a similar quantitative foundation is mostly lacking for the estimation of the nutritional resources needed for immunity. This is probably due to the complexities and uncertainties surrounding the process. Immunity is mediated by at least ten lineages of leukocytes that are located diffusely throughout the body. Nobel prizes are awarded almost annually for

fundamental advancements in our understanding of the immune system and its regulation. Clearly, it is difficult to evaluate, quantitatively, physiological systems that are incompletely understood and hard to locate.

Furthermore, the diverse types of challenges (e.g., viral, bacterial), the variable intensities and duration of the challenge (acute vs. chronic), and the differences in immune responses triggered by pathogens (e.g., innate, cell-mediated, humoral) make generalizations difficult. Nevertheless, several attempts have been made to determine the cost of immunity, including attempts to sum factorially the costs of the various processes of immunity (Lochmiller and Deerenberg, 2000; Klasing and Calvert, 1999; Cohn and Langman, 1990; Langman and Cohn, 1993). In our attempt (Klasing and Calvert, 1999), amino acids were used as the currency for estimating costs because the immunology litera-

ture is relatively replete with estimates of rates of protein accretion (e.g., antibody or acute phase protein synthesis) and cell proliferation; but there is a dearth of information on the energetics of these processes. Lysine, in particular, is used as the nutrient of choice for factorial summation of the costs of immunity because this amino acid has few uses other than as a substrate for protein synthesis.

Because we do not yet know all of the processes responsible for immunity, factorial summations necessarily underestimate the total costs. While incomplete and presumably providing an underestimate of the total cost of immunity, direct estimates provide important perspectives on the relative costs of different components of the system. As described below, the systemic acute phase response that accompanies an innate immune response appears to be the most expensive component of immunity in young chickens (Table 1).

Table 1 Relationship between types and costs of immune responses

Parameter	Developmental	Developmental	Maintenance	Nutritional	Effectiveness		Pathological
	time	costs	costs	costs of use	Novel challenge	Repeated challenge	costs of use
Non-specific immunity, including acute phase response	short	low	medium <sup>1</sup>	very high <sup>1</sup>	good	good	very high
Specific, lymphocyte-mediated immunity	long	very high	low	low	poor	excellent	variable <sup>2</sup>

1. Constitutive production of protective levels of complement, natural antibodies, and other broad-spectrum defensive proteins is considered as a maintenance cost. During an infectious challenge, rapid secretion of these proteins plus acute phase proteins has a high cost.  
2. Many of the pathological actions of specific immunity occur when immunoglobulins or T-lymphocytes activate macrophages and other cells of the non-specific system.

2.2 Indirect estimates

Because of the myriad of cell types, effector mechanisms and locations of the immune system, indirect estimates of the resources needed for protection have utility. Implicit in this approach is that the costs needed for immunity impinge on the nutrients available for other physiological processes. For example, the energy used by leukocytes during a response to a pathogen presumably siphons away energy for growth, reproduction etc. The decrease in energy deposited in growing or storage tissues that occurs during such a protective immune response should be proportional to the amount of energy utilized by that immune response. While indirect estimates of the costs of immunity are not particularly useful for identifying the relative contribution of various immune processes to the total cost, they circumvent many of the problems associated with our incomplete understanding of the process of immunity and availability of reagents to quantify the processes.

Though energy expenditure is the preferred currency for the measurement of many life history char-

acteristics, it has not always provided reliable results for studies on the cost of immunity. This is because there are many behavioral changes that accompany the immune response to pathogens which confound interpretation of changes in energy expenditure. For example, the acute phase response that accompanies immune responses to pathogens markedly decreases activity levels compensating for increases in energy expenditure attributable to immunity; the net result is little change in energy expenditure (Parmentier et al., 2002; Johnson et al., 1993). Indirect estimates of the developmental costs of immunity are not currently available, but indirect estimates for maintenance and use of the immune system have been made.

3 Costs of immunity development

The innate and adaptive arms of the immune system follow very different developmental schemes and, consequently, have very different developmental costs. In general, development of the innate immune system is gradual and efficient and has no obvious costs that distinguish it as being uniquely expensive.

Development of the adaptive immune system occurs through a notably inefficient process during a limited window of time, imposing a uniquely high cost.

3.1 Adaptive immunity

The receptors that lymphocytes utilize to recognize pathogens are generated via a series of semi-random recombination and point mutations in their coding genes within the thymus and bursa (Reynaud and Weill, 1996). This semi-random diversification is necessary to permit the immune system to recognize diverse pathogens and diminish evolution of their resistance. Diversification of antigen receptor genes typically results in ineffective receptors, which signal the deletion of the lymphocyte involved. Only rarely does a recombination event result in a functional antigen recognizing capability that does not recognize self-antigens too strongly. In these instances, that lymphocyte divides and migrates into the periphery where it populates lymphoid tissues and epithelia. In chickens, approximately 90% of developing B-lymphocytes and 95% of developing T-lymphocytes are non-functional and are deleted in the bursa and thymus, respectively (Reynaud and Weill, 1996; Lassila, 1989). This is the most inefficient developmental process occurring in the embryo and hatchling, and presumably it is energetically very costly.

Rates of protein synthesis and accretion within chicken bursa and thymus, rates of growth of the

thymus and bursa, and the rate of export of lymphocytes to the periphery permit estimates of the developmental costs of adaptive immunity. Rapid B-cell development starts at about E-14 and continues to about 4 weeks after hatching. The bursa expands from about 0.05% of body weight at E-14 to 0.45% of body weight at 3–4 weeks after hatching, when it reaches its maximum size (Betti and Sesso, 1989; Mercer-Oltjen and Woodard, 1987). At 4 weeks post-hatching, the bursa exports  $5 \times 10^8$  cells per day (Paramithiotis and Ratcliffe, 1994), representing 0.04% of body weight. The total lysine needed for expansion of bursa mass and cell export is 837  $\mu\text{mol}$ . During this same period, 75 950  $\mu\text{mol}$  of lysine are accreted in the whole body. Consequently, B-cell development accounts for about 1.10% of the lysine accreted in a growing chick (Table 2). The overall kinetics of thymus growth and T-lymphocyte migration to the periphery approximates that of B-lymphocytes; and the proportion of lysine accreted for development of the adaptive immune system is estimated to be about 2.2% (Klasing and Calvert, 1999). The rate of protein synthesis in the thymus and bursa are 2.4 and 3.6 times the whole body rate (Klasing and Austic, 1984) and, correcting for relative organ size, development of lymphocytes accounts for about 3% of the total daily energy expenditure used for protein accretion in a 4-week-old chick.

Table 2 Daily rate of protective processes and growth in young chicks<sup>1</sup>

Process	Normal		LPS challenged	
	Production (mg/kg/d)	Cost ( $\mu\text{mol}$ lysine/kg/d) <sup>2</sup>	Production (mg/kg/d)	Cost ( $\mu\text{mol}$ lysine/kg/d) <sup>2</sup>
Leukopoiesis in all tissues	650	45.5	1 300	90.9
Immunoglobulin synthesis <sup>3</sup>	114	65.6	121	69.6
Acute-phase protein synthesis	~0 <sup>2</sup>	~0	710	386
Total for immunocompetence	764	111.1	2 131	546.5
Body weight gain <sup>3</sup>	85 000	5 950	72 446	5 212
Lysine intake	–	9 520	–	8 311
% of intake used for immune processes		1.17		6.71
% of intake used for growth		62.50		62.70

1. From Klasing and Calvert (2000). LPS: Lipopolysaccharide.  
2. Constitutive production of complement and other defensive proteins is not included in this analysis because their synthetic rates are not yet available.  
3. For 2-week-old chickens.

Current theory on the diversification of the B and T cell receptor repertoire predicts that the number of lineages of functional lymphocytes that must be generated is independent of body weight (Cohn and Langman, 1996; Langman and Cohn, 1993; Cohn, 2000). This is because small birds are exposed to the same milieu of viruses, bacteria, and other parasites as large birds and must be able to recognize the same

number of foreign antigens. Thus all birds, regardless of size, are predicted to have similar absolute costs for diversifying their lymphocyte repertoires. Clearly, this cost represents a much larger investment for small birds than large. Presumably the only way that small birds can cope with these developmental costs is by either spreading them out over a long period of time or by accepting a smaller repertoire and poorer

capacity to recognize pathogens. Theoretically, birds smaller than 4 g cannot have a complete repertoire of lymphocytes because they lack sufficient space in their bodies for the number of cells required in each lineage to establish effectively protective levels of immunity.

### 3.2 Innate immunity

Cells of the innate immune system (e.g., macrophages and heterophils) utilize pattern-recognition receptors that are coded in the genome and do not require diversification or selection. As progenitor cells proliferate, all daughter cells are functional, express a full repertoire of pathogen-recognition receptors, and have equal utility in combating parasites.

The stem cells that give rise to cells of the macrophage-phagocyte system are present early in development and proliferate slowly, populating lymphoid organs as they are formed (Kent, 1961). Because of such straight-forward development, nutrients are needed uniformly during embryogenesis and are proportional to the number of innate immune cells in the embryo and hatchling. The number of granulocytes, monocytes and macrophages reach adult densities at about 1 week of age in chickens (Mast and Goddeeris, 1998; Jeurissen et al., 1992; Jeurissen et al., 1994), and account for 0.18% (14.4  $\mu$ mol) of the total of the 8.05 mmol of lysine accreted from E6 to 7 days of age (Table 2). Thus amino acid costs for development of the innate immune system appear to be relatively low. This simple and efficient development scheme, with all daughter cells competent, suggests that the energy requirements for this process would be low.

A hen makes a large investment in the innate immunity of her eggs and hatchlings. Chickens incorporate about 200 mg of immunoglobulin (IgY) into each egg yolk (Kowalczyk et al., 1985), which is about 3.8% of the egg's lysine. Furthermore, the antimicrobial proteins lysozyme, ovotransferrin, ovomucin, and avidin comprise about 25% of the egg white and function to protect the developing embryo (Romanoff and Romanoff, 1949).

## 4 Costs of immunity maintenance

The vast majority of lymphocytes in a healthy bird are "at rest" and are among the least metabolically active cells in the body. Their content of cytoplasm and RNA is exceptionally small, and rates of antibody secretion are negligible. Similarly, monocytes are not especially metabolically active unless they encounter a pathogen and are activated to differentiate into macrophages. A small fraction of B-lymphocytes differentiates into plasma cells which constitutively secrete immunoglobulin. The pool of constitutively secreting plasma cells includes lineages that have previously responded to a pathogen and lineages of B-1

cells that produce "natural antibody" that is especially important in constraining commensal microflora and clearing endogenous antigens. This constitutive secretion of immunoglobulin should be counted as a maintenance cost.

In the healthy adult, the immune system consists of a set of re-newing cell populations which continuously produce and lose cells in dynamic equilibrium. At maintenance, many of the cells of the immune system are relatively long-lived, with the exception of neutrophils. Replacement lymphocytes in immunologically mature animals result from the replication of lymphocytes in the existing pool. Consequently, each daughter cell is competent and the process of maintaining lymphocyte numbers is efficient. The liver is the primary accessory organ of the immune system and constitutively produces complement and other accessory proteins.

### 4.1 Direct estimates

The costs for maintaining the cells of the immune system can be put into perspective by examining the contribution of leukocytes and their effector molecules to body mass or body lysine (Table 2). The cellular elements of the immune system of an adult chicken contribute slightly less than 1% of the body weight. The primary effector protein in the body is Ig. In the chicken, total IgY, IgM and IgA (Leslie and Clem, 1970) comprise 0.13% of body weight and about 1.05% of total lysine content.

Though most leukocytes are very long lived, heterophils migrate into the intestines and IgA is secreted into the epithelia. At present, the cost of these losses is not known. Therefore, it is instructive to estimate the maintenance needs for the immune system from the rate of cell and Ig synthesis, assuming zero re-utilization of nutrients during replacement. The normal rate of immunoglobulin synthesis in chickens is about 0.025% of body weight per day (Leslie and Clem, 1970), which is 1.9% of the total lysine used by a 2-week-old chick. Leukopoiesis accounts for 0.76% of lysine use in a young chick. Based on serum concentrations and half-life estimates, it is likely that the amino acid demands for the synthesis of complement and other accessory proteins are an order of magnitude lower than that of Ig. Thus, the use of lysine for maintaining the immune system of a young chicken is likely to be less than 3% of the total.

### 4.2 Indirect estimates

Indirect estimates of the maintenance cost of immunity can be drawn from experiments examining chicks grown in a sterile environment relative to chicks grown in a conventional, but pathogen-free environment. Young chickens that have not been exposed to bacteria and viruses have far fewer leuko-

cytes, lower rates of leucopoiesis, and convert about 5% more of their dietary nutrients into body tissue than chickens in a conventional environment (Coates, 1973). Likewise, feeding high levels of antibiotics or antibacterials decreases the numbers of leukocytes, especially along the intestinal epithelium and spares about 5% of daily nutrient needs (Roura et al., 1992; Humphrey et al., 2002). These indirect estimates are somewhat higher than direct estimates (5% vs 3%) but confirm that the immune system has a measurable cost even when it is not being used to thwart pathogens.

## 5 Costs of immunity use

Any discussion of the costs of using an immune system requires a statement of the obvious: the pathology and necrosis induced by pathogens in immunodeficient hosts is usually fatal. On the other hand, a maximal response of the immune system may also be fatal (e.g., anaphylaxis or septic shock). Descriptions of the pathology induced by inadequate or excessive immune responses are detailed in every textbook on avian medicine, but estimates of the nutritional costs of a successful and appropriate immune response are poorly characterized.

The survival of an animal following infection by a pathogen is determined by the relative rate of pathogen proliferation versus the current level of protective immunity and capacity to recruit additional protection. Defense against novel pathogens is clearly more costly than re-engagement of previously encountered pathogens. The following analysis considers the costs of defense against a novel bacterial challenge. Most challenges begin with an influx of monocytes and heterophils from the blood to the site of infection and their secretion of effector molecules, such as reactive oxygen intermediates, lysozyme, complement and defensins. These phagocytes must be replaced by increased output from leukopoietic areas of bone marrow. Stimulated leukocytes release interleukin-1 $\beta$  (IL-1 $\beta$ ), IL-6, tumor necrosis factor- $\alpha$ , and  $\gamma$ -interferon. These cytokines orchestrate a systemic acute phase response that includes fever, anorexia, and recruitment of the vast immune defense capabilities of the liver, especially the secretion of acute phase proteins (Parmentier et al., 1993; Klasing, 1998a; Adler et al., 1998; Johnson, 1997; Johnson et al., 1993). Over the next few days, B and T lymphocytes that recognize antigenic determinants on the pathogen begin to proliferate. The responding lymphocytes form germinal centers in nearby lymphoid tissues where affinity maturation of Ig occurs. After about a week, plasma cells begin to produce protective levels of Ig, and T-cytotoxic lymphocytes seek out infected host cells and kill them.

Most novel pathogens induce strong innate and adaptive immune responses, and costs of immunity must take both into account. Experimentally, many investigators use purified antigens like KLH, BSA or SRBC, which do not stimulate robust innate immune responses and are poor model systems for true infectious diseases. However, reagents that selectively stimulate either a B-lymphocyte response or a T-lymphocyte response are instructive in itemizing the specific costs of various arms of the immune system.

### 5.1 Direct estimates

The costs of using the immune system are equal to the increase in cell proliferation and secretion of effector molecules triggered by a pathogen (Table 2). Following a successful immune response, the number of leukocytes and levels of effector molecules return to normal and the nutrients left over are presumably redirected to other uses.

**5.1.1 Innate responses** The infiltration of leukocytes during the first day of a simulated peritoneal infection results in the accumulation of about  $1.5 \times 10^8$  macrophages and heterophils per kg body weight (Golemboski et al., 1992; Klasing, 1998a; Sabet et al., 1977). This is equivalent to about 0.0025% of total body weight. In large mammals, fever has a considerable energetic cost, but in chickens and other birds, a net change in energy expenditure due to fever is not normally observed because of compensatory decreases in other expenditures such as activity, growth or reproduction. The accretion of acute phase proteins (Barnes et al., 2002; Adler et al., 1998) is the single most significant use of amino acids during an immune response, accounting for 386  $\mu$ moles of lysine/kg/d or 4.6% of the lysine intake in a 3-week-old chicken. Clearly, the recruitment of liver action away from its normal functions in secreting nutrients to support growth or reproduction to aid immune defenses is the single most expensive component of immunity to pathogens that induce an acute phase response.

**5.1.2 Adaptive responses** Acute systemic infections in mammals causes a 2-fold increase in the rate of leukopoiesis in bone marrow (Elgert, 1996) to 0.06% of body weight per day; but corresponding information for birds is not available. The rate of synthesis of Ig specific for epitopes on pathogens increases remarkably during an infectious challenge, from levels that are often undetectable to effective concentrations of between 10 and 100 ng of Ig per ml of extracellular fluid (Cohn and Langman, 1990) in less than a week. The total amount of antigen-specific-Ig produced following hyperimmunization of complex antigens augments plasma Ig levels by about 25% in chickens (Leslie and Clem, 1970). Assuming that a similar increase in Ig occurs in all extracellular fluids, this represents an increase of about 28 mg of Ig per

kg body weight per day. In chickens challenged with a highly antigenic protein, the influx of lymphocytes into the spleen and the formation of germinal centers accounts for only about 0.01% of body weight (Humphrey and KLASING, unpublished observations).

In most challenges by novel pathogens, the innate response precedes the peak adaptive response and the expenses of the two arms are spread sequentially. Only in the case of persistent pathogens can both innate and adaptive arms of the immune system be expected to respond simultaneously at high levels. The above accounting indicates that the amount of lysine needed to support such a simultaneous response is 550  $\mu\text{mol/kg/d}$ . If this quantity were to be used for growth, it would support the accretion of 7.8 g of body mass/kg of body weight.

### 5.2 Indirect estimates

Indirect measurements of the cost of a vigorous immune response have been obtained by exposing growing chicks to bacterial lipopolysaccharide (LPS). LPS induces an intense innate and adaptive immune response simultaneously by stimulating macrophages, B-cells and T-cells through specific LPS receptors. Under this model system, growth rate slows from 85 g/kg/d to 72.4 g/kg/d in young chickens (KLASING et al., 1987; BENSON et al., 1993). Interestingly, known process in immunity can account for about 60% this loss (Table 2); and most of the remainder is due to anorexia.

The high cost of an acute phase response probably explains why a variety of avian species respond to challenges from live bacterial and viral pathogens, and sometimes even relatively benign parasites, with changes in body condition and energy metabolism that are much greater than can be accounted for by summation of the substrates needed for adaptive immune responses (SHeldon and Verhulst, 1996; Martin et al., 2003; Korver et al., 1997). Even benign antigens like red blood cells in sheep stimulate a mild acute phase response that can be measured as increased heat production, protein turnover, fever, and slightly decreased rate of growth (Cook et al., 1993; KLASING and Austic, 1984; KLASING et al., 1987; Siegel et al., 1982a). The idea that an immune response diverts nutrients away from growth, reproduction and other productive purposes needs to be put into context. A quantitative analysis of the processes involved indicates that anorexia and changes in nutrient use by the major organs of a bird, especially the liver, are primarily responsible and that use of nutrients by leukocytes is only a minor contributor.

Although the above analysis has focused on model systems that invoke vigorous immune and acute phase responses, frequent challenges of low intensity can, over long periods of time, result in diminished

productivity. For example, the frequency with which the immune system responds to challenges by opportunistic microorganisms is inversely proportional to the rate of growth and the efficiency of dietary energy use for tissue deposition. Hatchling chickens housed in environments where they have frequent but low level challenges have greater numbers of leukocytes present along their epithelia; presumably the cost of sustaining this higher level of surveillance amounts to about 5% of daily nutrient use (Roura et al., 1992; Humphrey et al., 2002).

## 6 Conclusions and predictions

All avian species require an immune system that is sufficiently competent to thwart the continuous challenges from commensal microflora and occasional challenges by true pathogens. However, immunity comes at a cost that must be paid at the expense of other processes, and it is unlikely that any species, or individual, possess the maximum immunity possible. Presumably there is a continuum of levels of investment for immunity at the species level, and that factors related to environment and life history drive this variability. Our current view of the avian immune system is colored heavily by what happens in the chicken. The chicken immune system is very different from that of mammals. In the few instances where other avian species have been examined, albeit superficially, surprising diversity has been found. For example, ducks produce a structurally and functionally different IgY to that of chickens, and the production of this unique effector molecule affects the cost of immunity markedly (Higgins, 1996; Humphrey et al., 2001). There is reason to expect that even greater diversity will be found as attention is focused on other orders that have greatly different body sizes, life-histories, and phylogenies.

Given that each component of the immune system has a unique cost and benefit, it is likely that there is a wide variety of strategies for immunity (Ricklefs and Wikelski, 2003; KLASING and Leshchinsky, 1999). Each strategy may accentuate specific components of immunity and de-emphasize others. Developmental costs are uniquely high for lymphocytes, and the rewards of owning a robust repertoire may not be sufficient in some species. Recombination, gene conversion, and mutation processes necessary for generating a diverse repertoire of lymphocytes expressing unique antigen receptors takes several months to develop and are a major cost to the chicken in terms of both time and energy. Presumably, some species forgo this expenditure and have a narrow and incomplete repertoire of lymphocytes that would result in lower probabilities of recognizing some pathogens as foreign. At the other end of the contin-

uum are species that invest resources to develop a robust repertoire of lymphocytes that can recognize nearly all potential pathogens and provide maximal protection.

Current knowledge predicts that species with long life spans will invest more time and nutrients into developing a robust repertoire of lymphocytes (Ricklefs and Wikelski, 2003; Klasing and Leshchinsky, 1999). Species with a long life span and slow reproductive turnover will be disproportionately affected by mortality from the rare pathogens that cannot be recognized by their innate immune system. Additionally, the longer an animal lives, the less likely that a pathogen challenge will be novel and the greater the benefit of memory for specific, lymphocyte-mediated immunity. Thus long-lived species receive more benefit from specific immunity and are more likely to invest more in this component of the immune system.

Once developmental processes are complete, species may invest differing amounts of nutritional resources into maintaining pools of leukocytes ready to respond to challenges by pathogens. For example, levels of some immunoglobulins are maintained at sufficiently high levels to provide immediate protection (Cohn and Langman, 1990). These so-called “natural antibodies” are only a subset of the total repertoire but are very important in determining resistance (Flajnik and Rumfelt, 2000; Boes, 2000; Cotter, 1998) and represent one of the largest components of the maintenance costs of immunity. There appears to be considerable species variability in the number of clonotypes represented in basal levels of circulating Ig, and this may represent differing levels of investment in maintaining specific immunity. Given the importance of constitutive Ig production in managing commensal microflora populations, it might be expected that species with large caeca may invest more in maintenance function.

An immune response to a pathogen requires clonal proliferation of lymphocytes, formation of germinal centers, recruitment of new phagocytes from bone marrow, and synthesis of effector molecules (e.g., lysozyme, complement). Most immune responses are also accompanied by a systemic acute phase response, which has an exceptionally high cost. Though blocking the acute phase response impairs resistance to some types of pathogens, the protective value of the acute phase response is thought to be relatively low and non-specific compared to leukocyte-mediated effector functions. Consequently, the acute phase response might be considered to have a low benefit to cost ratio, and be de-emphasized in some life-history strategies. Among chickens bred for differing rates of growth, we have detected differing investments in

the acute phase response, with faster growing strains having a blunted response (Leshchinsky and Klasing, 2001). The balance between investment in adaptive immunity during development and reliance on “pay as you go” innate immunity will presumably follow predictable patterns related to life-histories. So uncovering their relationships to life-span, mode of development, dietary preferences, habitat preferences and reproductive strategy should be instructive.

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## Adaptation of birds to life in high mountains in Eurasia

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**Abstract** The paucity of the avifauna of the Eurasian highlands (only 75 species breed regularly above the timber line) is determined by severe natural conditions and scarcity of food sources. Principal adaptations to meet these conditions are in modes of flight, including morphological peculiarities connected with them, choice of time of breeding and nesting places which optimize use of microclimate and camouflage, limitation of clutch size, mode of transportation of food to nestlings, and protection from strong ultraviolet radiation and atmospheric desiccation. Most life history characteristics of Eurasian highland bird life need further research [*Acta Zoologica Sinica* 50 (6): 970–977, 2004].

**Key words** Ecological adaptations, Eurasian highlands, Flight, Breeding

## 鸟类对欧亚地区高山生活的适应

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**摘要** 欧亚地区高地鸟类区系的贫乏性（仅有 75 种繁殖于林线之上）受严酷的自然条件和食物资源短缺所决定。适合这些条件的主要适应是飞行模式，包括与之有关的形态特征，繁殖时间的选择，最优化利用微生境和伪装的巢址选择，窝卵数的限制，对雏鸟的食物转运模式，防护强紫外线辐射和大气干燥。大多数欧亚高地鸟类的生活史特征有待于进一步研究 [动物学报 50 (6): 970–977, 2004]。

**关键词** 生态适应 欧亚高地 飞行 繁殖

### 1 Introduction

The highlands of Eurasia, covering 2.5 million km<sup>2</sup>, are the largest in the world. The area above 4 000 m a. s. l. is also 2.5 times larger than on all other continents. Covering more than 90% of that area is the Tibetan Plateau and its surrounding mountain systems. Accordingly, the scope of this paper centers mainly on the bird fauna of that uplift. There is no general text covering this topic, so I have drawn on my own data from six seasons on the Pamir Plateau (Potapov, 1966 a, b), my research on other mountains in Eurasia (Alps, Caucasus, Elburs, Tian-Shan, Alai, Russian and Mongolian Altai), and scattered data on high mountain species from many published papers.

The terms “highlands” or “high mountains” that I use here apply to the sub-alpine and alpine zones or belts between the timber-line and the snow-line. On mountain ridges, these zones are confined to rather narrow strips, but on high plateaus and the transitional ground between plateaus and ridges they cover huge areas. Wherever they occur, they are open and

exposed and lack trees and bushes. The upper border of the zone is the snow-line and is clearly defined. But the lower border—the timber-line—is not so clear-cut. In the wetter mountains where the forest belt is well developed and the timber-line intact, it occurs at heights from 2 000 m (Alps) up to 4 500 m (Himalayas), depending of geographical latitude, regional climatic conditions and exposure of the slope. On many central Asian ranges, however, the forest belt is absent because climate is too dry. In such cases, the lower border of the highland zone is determined by the lower limit of plant communities typical of sub-alpine conditions, or by the upper limit of arboreal vegetation along streams (Staniukovich, 1960).

In mountains with warm and humid climates (e. g., the western Caucasus and especially the southern Himalayas), the upper border at the snow-line can reach 5 000 m (Schafer, 1938). Despite their great altitude above sea level, however, I do not treat these areas as highlands because of their extensive penetration by forest avifauna: such species do not spread to open landscapes of the Eurasian highlands generally. Rather, birds considered here to be members of the

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Eurasian highlands fauna are those which inhabit the open high mountain zone above the tree- or the bush-line. In this zone, natural conditions are so unfavorable for bird life that only 75 species breed there, 24 of which nest nowhere else. These are the real en-

demics of the Eurasian highlands and are the most ancient elements of its avifauna (Table 1); and because of this, their adaptations to highland life are especially interesting.

**Table 1** Birds endemic to and breeding only in the Eurasian highlands

Species	Altitude (m)	Species	Altitude (m)
<i>Tetraogallus caucasicus</i>	2 450 – 3 500	<i>Prunella himalayana</i>	3 200 – 4 700
<i>Tetraogallus tibetanus</i>	3 600 – 5 500	<i>Phoenicurus erythrogastrus</i>	2 200 – 5 500
<i>Perdix hodgsoniae</i>	3 700 – 4 800	<i>Grandala coelicolor</i>	4 250 – 6 600
<i>Lerwa lerwa</i>	3 300 – 5 500	<i>Saxicola insignis</i>	2 200 – 3 000
<i>Lyrurus mlkosiewiczzi</i>	2 200 – 3 100	<i>Pseudopodoces humilis</i>	3 200 – 5 200
<i>Grus nigricollis</i>	4 300 – 5 300	<i>Pyrgilauda taczanowskii</i>	4 000 – 5 300
<i>Larus brunnicephalus</i>	3 200 – 4 800	<i>Pyrgilauda ruficollis</i>	4 000 – 5 100
<i>Columba leuconota</i>	4 000 – 6 000	<i>Pyrgilauda blanfordi</i>	4 150 – 5 100
<i>Syrrhaptes tibetanus</i>	3 300 – 5 700	<i>Leucosticte brandti</i>	3 400 – 5 700
<i>Melanocorypha maxima</i>	3 500 – 6 000	<i>Carpodacus rubicilla</i>	2 500 – 5 000
<i>Eremophila teleshowi</i>	3 200 – 5 500	<i>Pyrrhospiza punicea</i>	3 200 – 5 200
<i>Anthus roseatus</i>	4 000 – 5 300	<i>Kozłowia roborowskii</i>	4 600 – 5 600

The low level of endemism reflects the comparatively young age of the highlands in general, at no more than 1 – 2 million years. It is interesting to note that the first scientist to analyze the highland fauna was the famous zoologist, P. Sushkin. In his work, published in 1928, he showed that its formation was a slow process, closely connected with the gradual uplift of large terranes with their original fauna. The arboreal avifauna disappeared together with arboreal vegetation when the rising mountains reached altitudes too high for tree growth, where species adapted to open habitats now had more opportunities to survive. In the highland avifauna of today, nearly all species are those of open habitats; birds originating from arboreal avifaunas are the exceptions (Kozlova, 1952).

## 2 Environmental characteristics

In mountains, annual average air temperature decreases 1 degree C for every 170 m; thus average annual temperature is zero degrees centigrade at 4 700 m a. s. l. at the equator. Given their near-freezing average temperature, the Eurasian highlands are still more unfavorable to birds environmentally than high arctic regions due to a combination of factors unique in terrestrial ecosystems. Those factors are low levels of oxygen and its rarefaction, low atmospheric pressure, high rates of solar radiation, high levels of evaporation and consequent ultra-low humidity, and vertically structured landscapes.

The environmental contrasts between lowlands and highlands can be pronounced. For example, two

valleys in Tadjikistan near 38 degrees N, which are separated by only 360 km horizontally but 3 600 m altitudinally, look like two different worlds. The Wahsh River valley, at only 400 m a. s. l., has a dry subtropical climate (average air temperature + 17 °C in January), with rainforest on the river flood plain and a rich flora and fauna. In contrast, the Alichur River valley at a height of 4 000 m a. s. l. has an average air temperature of only – 27 °C in January and + 12 °C in July, with just 45 days without frost in summer and a plant growing season of only 70 days. Covered with marshy alpine meadows, it has no trees or shrubs and is exposed every day to strong cold winds; only at dawn is the wind calm.

Low ambient temperatures and high levels of evaporation create a permanent deficiency of moisture in the Eurasian highlands. Moisture deficit not only prevents the development of arboreal vegetation, but also gives the landscape the appearance of a permanent cold desert, a specific highland ecosystem characteristic of the high plateaus of central Asia (Tibet, Pamir, Ladakh etc.). Natural condensation and precipitation partially compensate for the lack of moisture, but they are insufficient in most of the central highlands because high mountain ridges surround them and create rain-shadows.

The scarcity of vegetation that results is also unfavorable for birds. Patches of sub-alpine and alpine meadows occur as no more than boggy fragments along rivers, around lakes, at bottoms of glacial cirques and in wet pockets on slopes. In most other places, ground surface is nothing more than bare

stony or sandy soil, sparsely dotted with grasses and dwarf shrubs. Under these conditions, food is scarce, accounting in turn for a paucity of bird life. Thus, although the Palearctic zoogeographical region is inhabited by 937 species of birds, and the adjacent Indo-Malayan region by another 1 270, only 75 species from both these regions occur and breed regularly in the Eurasian highlands.

Some environmental phenomena, nevertheless, do make this severe habitat more comfortable for birds. One is strong solar irradiation by day, even in the winter. As a result, temperatures on open surfaces can reach  $+10^{\circ}\text{C}$  in January and  $+54^{\circ}\text{C}$  in July. High irradiation and a short plant growing season intensify all vegetative processes. Alpine plants concentrate considerable quantities of nutritious components before the onset of winter, such that the nutritious value of highland plants is significantly higher than in lowland ones (Iusov, 1958). Another favorable feature comes in winter. Despite the severity of the weather then, the highlands are still more equable for birds than the tundra zone because they lack the long polar night. Moreover, the snow cover on inner parts of the highlands, especially on the southern slopes of the ridges, is often either absent or thin and fragmented.

Such environmental complexity of different temperatures, air and substrate moistures, rather constant wind, and other climatic factors and features of relief, creates a considerable diversity of micro-climatic variability in this biome. These pose several important challenges and opportunities for birds (and other animals), such as the best sites for nesting, feeding and roosting etc. In most cases, habitats favorable for a particular species are usually highly fragmented and isolated from one another. The distance may vary from a few hundred meters to several kilometers; and sites teeming with birds may be separated by vast areas with little or no bird life.

### 3 Adaptations

#### 3.1 Avian physiology and altitude

To the question of to what degree do the properties of highland atmosphere (rarefaction of air etc.) affect birds negatively, it is known that air at 4 000 m a. s. l. is only about half as dense as at sea level. It seems, nevertheless, that birds do not have serious problems with reduced air pressure. Adaptations to flight at high altitudes, such as ability to fly in air of low oxygen content and low atmospheric pressure, and to compensate quickly for sudden changes in altitude, are widespread in birds and not unique to highland species. In fact, this adaptation has made diverse aspects of avian flight possible! Many bird species that breed in the tundra and taiga of lowland north

Eurasia migrate regularly twice a year over the highlands, even crossing the highest mountain ranges. According to my own data and that of many others, large birds, such as cranes, geese and ducks, have been reported flying at altitudes of more than 9 000 m a. s. l., and many smaller birds, mostly passerines and waders, at above 6 000 m. Most of these birds not only cross the highlands easily, but may stay in elevated areas for several days or even weeks for stopover rests and feeding.

Sudden snowstorms and snowfalls may pose serious problems, but for birds migrating across high mountains, low atmospheric pressure and lack of oxygen are the norm and present no difficulties. Many non-breeding birds, moreover, spend their summer months on highland lakes and other wet areas, e. g. cormorants, sea eagles, ducks, plovers etc. Some birds also reach very high altitudes during hunting flights, vultures climbing to more than 11 000 m on occasion (Layborne, 1974). Recent experiments (Tucker, 1968; Irisov, 1997; Leon-Velarde et al., 1997; Mathieu-Costello and Agey, 1997) have shown that birds can adapt rather quickly to low oxygen levels at high altitudes, even during a single life span. No wonder then that 51 of the 75 species that breed in the Eurasian highlands also dwell at low altitudes down to sea level and even below, in the Caspian and Turfan depressions; the other 24 species breed only in highlands (Table 1).

#### 3.2 Flight

What are the main adaptive attributes that help birds to live at high altitudes? First of all, flight. Rarefied air in highlands, vertically structured landscapes and permanently strong winds are not favorable for flight. In response, many species, mainly insectivorous passerines, prefer habitats protected to some degree from winds, while others limit flying activity as much as possible, such as larks that sing on the ground or in the air only during brief spells of calm. Some birds even seem to flatten themselves against rocks or any other surface to escape the effect of wind when searching for food, such as the wall-creeper *Tichodroma muraria*, and Hume's Tibetan jay *Pseudopodoces humilis*. Yet there are many birds which are strong fliers and fly in any direction and at any height regardless of the wind. Among them are the Mongolian plover *Charadrius mongolus*, several pigeons, Brandt's rosefinch *Leucosticte brandti* and the grandala *Grandala coelicolor*, as well as birds of prey, geese and ducks.

All highland birds need to undertake numerous flights everyday to cover often considerable horizontal and vertical distances between feeding, nesting, roosting, and sheltering sites. In the process, they instinctively use all means available to them to save

energy. Help is provided here by two natural forces: (1) thermal up-wellings of air for upward flight, especially along mountain slopes in daytime, and (2) gravity for downward flight. Different species use these forces in different ways, an outstanding example being the choughs (*Pyrhocorax* sp.). Their main feeding sites are the boggy sub-alpine meadows in valley bottoms; and when they quit the feeding areas, they leave by conventional flapping flight until reaching the nearest mountain slope. There they catch thermal updrafts and start to ascend by soaring, rising to heights until they are practically invisible from the ground. From this level, they then begin to descend toward nesting or roosting sites by gliding, dropping by the force of gravity. In such a way, the birds cover distances of 10 and more km without a wing stroke. The wings are spread wide in upward soaring and partly folded in downward gliding.

One of the largest mountain birds of prey, the lammergeier or bearded vulture *Gypaetus barbatus*, exemplifies the use of soaring flight in hunting. In contrast to the choughs, it soars on thermal up-streams close to mountain slopes (sometimes not higher than a dozen or so meters) during breeding, searching mainly for marmots. Marmots are wary, far-sighted rodents and while feeding do not move far from their burrows; if alarmed, they quickly run back to their holes giving loud warning whistles. To approach marmots undetected, lammergeiers take them by surprise using a ridge-hopping technique: they soar up along the slope to the crest of a ridge and then cross to appear suddenly over the marmot colony on the slope on the other side. Surprised marmots have no time to reach their burrows and are seized.

Brandt's rosefinches also exploit the force of gravity. This highly specialized high mountain endemic is one of the most common passerines in the Asian highlands. Rosefinches breed and roost only on steep slopes under stones or in rock crevices and holes at very high altitudes close to the snow line. No larger than a sparrow (weight nearly 30 g), they perform daily up and down flights between nesting and feeding sites. Feeding habitats are the patches of alpine meadow at the bottoms of valleys and creeks above the tree line; and so the vertical distance between feeding and nesting sites can be as much as 1 000 m at the beginning of breeding. When flying downhill, rosefinches descend on a very steep trajectory—at up to 80 degrees, close to a vertical drop—but not in a straight line. Whenever the velocity of the drop becomes too great, the birds slow their speed with the help of their wings, adjusting them to a greater angle of attack and simultaneously spreading them in several beats. This changes the angle of flight trajectory momentarily to close to horizontal, stopping the birds

as if they had met an invisible obstacle; and so velocity decreases. The sequence is then repeated over and over until the birds reach their feeding grounds. During the periods of gliding, the wings are half folded as in a stooping falcon.

The return flight with food for young is much harder work, especially for parents carrying large quantities of food, up to nearly 15% of body weight. They fly up along the slopes with frequent stops of several seconds for every 70–100 m of the journey. I observed the same strategy in the daily flights of nesting desert wheatears *Oenanthe deserti*, Guldenstadt's redstart *Phoenicurus erythrogaster* and some others, though it was not so well-marked. Another similarly specialized highland bird is the grandala, an insectivorous thrush. Its lower limit of nesting is well above the timber-line, and, like Brandt's rosefinch, it forages for food for its young in sites hundreds of meters below the nest, requiring regular daily up-and-down flights. The shape of its wing is the same as in Brandt's rosefinch, and the mode and strategy of daily flights during the nesting period may be the same too, though no proper studies have yet been carried out to test this. The grandala is one of the less familiar high-mountain birds.

Gliding flight is developed to extremes in all 5 species of snowcocks (*Tetraogallus* sp.), two of which are highland endemics. These heavy gallinaeous birds (2.2–3.5 kg) inhabit steep mountain slopes, and their daily routine takes them down on wing to their feeding grounds in the morning, and then back up to roosting and nesting sites during the day on foot. In adapting to life on steep slopes over hundreds of thousands of years, they have lost horizontal flapping flight and cannot take off from a horizontal surface; to become air-born, they need a downward slope. They take off from such slopes with a strong leg thrust and a few energetic wing beats, after which gliding begins immediately on a slow descent. In the Pamir Mountains, I recorded snowcocks covering about 1.5 km during glides from one slope to another, losing 400 m in height but regaining 100–120 m again before landing. Height regained prior to landing occurs when the bird decreases its speed with its wings by adjusting them to a greater angle of attack. The force of inertia (large body mass combined with high speed) generates lift that allows the bird to regain some altitude just before the moment of landing.

Adaptation to this mode of flight is reflected in the external and internal morphology of the flying apparatus in snowcocks. The weight of primary flying muscles (*M. pectoralis major*, *M. coracoideus*) constitute only about 15% of body weight, quite minimal relative to the weight of these muscles

throughout the order Galliformes. The sternum is also of minimal depth, with a height only 25% of its length. A unique feature of snowcock wing morphology is the right angle between the humerus and ulna; in other species of partridges (e. g., rock partridge *Alectoris kakelik*), this angle is about 120°. As a result, the snowcock wing is proportionally wider and significantly shorter than those of its relatives, proportions achieved nevertheless with bones of the same length. An enlarged propatagial area results, accounting for great strength in the wing. The propatagium helps to absorb the high pressure on the wing during gliding flight at speeds exceeding 80 km/hour. Body mass alone gives a loading of 1.7–2.3 g/cm<sup>2</sup>—the maximum in Galliformes and perhaps flying birds in general. This adaptation of the wing enables snowcocks to live in high mountains anywhere up to the snow-line (Potapov, 1992). It is important to bear in mind, however, that high altitudes are not essential for snowcock flight, the birds living comfortably in mountains at altitudes down to 700 m in the Altai. But snowcocks do need open steep slopes of not less than 300 m of vertical distance from top to bottom for effective flight.

### 3.3 Breeding

Other important adaptations in highland birds are associated with breeding. Breeding success depends on behavioral strategy; the bird must choose the optimal time, both with respect to temperature for rearing young and synchronization with the maximum abundance of food. The latter is especially important in highlands, where food resources are commonly scarce; and the birds also need to choose the best place for hiding nests in a position as close to feeding grounds as possible.

Cold climatic conditions are the main reason for later breeding seasons in most high mountain birds. On the Pamir Plateau (38°N), for example, the breeding season for insectivorous species begins at the end of May, later than in the northern taiga at 65°N. Some birds with prolonged incubation and nestling periods, such as large raptors or the raven *Corvus corax*, are forced to breed at lower altitudes, where spring-summer warmth is longer and begins earlier. In contrast, birds with shorter and especially later breeding times can nest at higher altitudes up to the snow line. Many of these are finches that begin to breed synchronically with seed-ripening in alpine grasses when day-length begins to decrease after the summer solstice, a phenomenon that also applies to lowland seed-eaters in the Palearctic. Practically all highland finches, such as Brandt's rosefinch, the twite *Cannabina flavirostris*, great rosefinch *Carpodacus rubicilla*, red-breasted rosefinch *Pyrrhopiza punicea* and Mongolian trumpeter finch *Bu-*

*canetes mongolicus* adjust the rearing of their young to the stage of maximum ripeness of grass seeds.

Choosing nest sites with not only optimal microclimates, but also well hidden from predators is another problem to be overcome. All highland birds that hide their nests prefer sites under stones on slopes or in rock crevices and holes. Those species that nest on open flat surfaces need, in contrast, ground-matching camouflage. Not surprisingly, the majority of highland birds nest on mountain slopes and under rocks or in crevices; only 15 species nest on flat or slightly hilly bottoms of valleys, lake depressions or islands in lakes. In such areas, the soil surface is almost barren, no more than very sparsely vegetated with occasional grasses and "cushions" of dwarf bushes up to 15–20 cm high. Only a fraction of these flat areas is taken up by swampy meadows along the banks of lakes and rivers. Bare islands and swampy meadows are used for nesting by waterfowl and shore birds, such as the bar-headed goose *Anser indicus*, ruddy shelduck *Tadorna ferruginea*, common redshank *Tringa totanus*, Tibetan crane *Grus nigricollis*, brown-headed gull *Larus brunnicephalus*, citrine wagtail *Motacilla citreola* and several others. All these species are attracted by plentiful water, which is otherwise in short supply in the highlands, and by a thick grass cover rich in invertebrate animal life. The redshanks, wagtails and larks that nest in swampy meadows use tall grass cover to hide their nests. Others (geese and gulls) find protection from raptors by nesting colonially on islands.

The patches of marshy meadows are as oases surrounded by barren flatlands, which occupy most of the ground in valleys and accommodate only five species that nest in such situations: Tibetan sandgrouse *Syrhaptes tibetanus*, Mongolian plover, horned and Tibetan horned larks (*Eremophila alpestris*, *E. teleschowi*), and Hume's short-toed lark *Calandrella acutirostris*. They avoid steep mountain slopes and share a similar hatching schedule correlated with, and dependent on, the heat of the sun. The birds stay on their eggs almost round the clock, protecting the clutches from the night cold and the midday heat when temperatures are sufficiently extreme to damage the embryo. Nestlings in open nests are also exposed to strong ultraviolet radiation. Well-developed dark pigmentation of the skin in the nestlings might well act as protection here. Such pigmentation is well expressed in the young of the Tibetan sand grouse, horned lark, Hume's short-toed lark and brown accentor *Prunella fulvescens*, and to a lesser extent in the common redshank, brown-headed gull, Tibetan common tern *Sterna hirundo tibetana* and citrine wagtail. This phenomenon, however, needs further study.

Opportunistic predators, such as ravens and choughs, are a particular problem for birds with open, exposed nests. How can the nest be hidden? Here camouflage is the main protection. For example, Tibetan sand-grouse and Mongolian plover, which lay their eggs straight on a scrape in the ground, have camouflaged plumage, nestlings and eggs which are all practically invisible against a background of soil and stones. Tibetan common terns use the same strategy when nesting solitarily on barren islands; yet if they nest in colonies with gulls, and so under their protection, they build the real nests. Larks nesting in exposed sites create well-camouflaged nests, usually placing them in small hollows in the ground dug by the birds themselves in positions where the nest is usually protected from prevailing winds by a stone or dwarf shrub. Fresh soil particles excavated in the process can be conspicuous on the surface of sun-scorched soil. To overcome this, the birds disguise such debris by covering it with small flat stones and pieces of soil crust. Such camouflage can resemble stone-paving.

Other birds cope with problems of exposure and predation by nesting in the burrows of marmots and pikas. Among them are the ruddy shelduck, isabelline wheatear *Oenanthe isabellina* and three species of snowfinches: rufous-necked, plain-backed and white-rumped (*Pyrghilauda ruficollis*, *M. blanfordi* and *M. tacanowskii*). Another species that nests in burrows—Hume's ground jay *Pseudopodoces humilis*—digs its own holes. Burrow nests need no camouflage but are still not protected from foxes or stoats. Even so, predation pressure is not heavy on birds in the Eurasian highlands, and, indeed, is one of the favorable factors for them. There are no raptors that specialize on birds; most of them (except for the Himalayan griffon *Gyps himalayensis*) take mostly rodents and lagomorphs instead. Other animals that might prey on nests, such as snakes, jays, magpies, squirrels etc., are largely absent because of low temperatures and scarce vegetation cover. Only the numerous choughs exert much pressure on the nests of small passerines.

The majority of highland birds place their nests on mountain slopes—under boulders and stones on steep slopes or in cliffy terrain, especially in rocky canyons or groups of rocks where the birds use crevices, holes and cavities. It is well known that shifting from nesting in trees and bushes to among rocks or under stones is not difficult for many species. The gradual uplift of the mountains over hundreds of thousands of years, which was accompanied by the progressive disappearance of arboreal vegetation at higher altitudes, gave birds enough time to change from traditional nesting in trees and bushes and adapt

to new sites under stones or in rocks above the lowering tree-line. Some species even use both types of site opportunistically, especially near the upper limit of arboreal vegetation: common kestrel *Falco tinnunculus*, brown accentor, twite and others.

The diversity of sites for rock-nesting in the highlands also offers a wide selection of microclimates for the comfort of nesting birds and their young. Crevice microclimates are affected mainly by the exposure of cliff or slope, and the direction of prevailing winds. Another important factor is humidity. The low humidity of highland climate is as important a factor as temperature because embryos can dehydrate due to strong evaporation through egg-shell. Humidity is often the critical factor in the choice of a nesting place among rocks for *Columba leuconota*, *Pyrhoxorax graculus*, *Prunella collaris*, *P. himalayana*, *Leucosticte brandti* and others. A common feature of rock- and slope-nesting is its positioning above the main feeding grounds of the birds. This is largely because food resources become less abundant with increased altitude, while the number of suitable and safe places for nesting increases. The vertical distance between these sites usually varies from a dozen to several hundred meters, and can reach a kilometer or more for the grandala and Brandt's rosefinch. Even such waterfowl as the bar-headed goose, ruddy shelduck and great merganser *Mergus merganser* prefer to nest among high rocks at 500–600 m above the bottoms of valleys, because of safety and higher humidity. The downy young of these species are able to jump out and drop down tens of meters on to bouldery slopes from such nests without damage; and after this they are herded by their parents to the nearest water, covering distances of sometimes more than a kilometer on foot.

Microclimatic conditions are rarely perfect at the nest site, requiring most birds to build very thick and warm nests. Many passerines weave considerable quantities of wool and feathers into the walls and cups of their nests, which are considerably thicker than those of the nests of birds living at lower altitudes. In the highlands, wool is available from the molting of wild and domestic mammals. Sometimes all the space within the nest hollow is completely filled with insulating material. As a result, incubation is not a problem despite frequent cold snaps, including snowfalls. All my measurements of nest temperature in 11 bird species nesting under different conditions demonstrated that temperature in the nest chamber was always at least 4–5 °C higher than the external, never dropping to zero even in the semi-exposed nests of snowcocks. It must be pointed out, too, that practically all 150 nests that I examined above 3 800 m a.s.l. on the Pamir Plateau were placed on slopes and

among rocks with exposures to the south or south-east, except for the nests of Brandt's rosefinch. The temperatures that I have measured inside these nest shelters at 4 750 m a. s. l. was constantly higher, at about 4 – 12 °C, than ambient temperature outside, which may reflect the effect of temperature inversion so usual in the highlands. The nests of this species in the Pamir do not have very thick walls and may or may not have thin insulating layers of wool, further evidence of good temperature conditions inside nest shelters.

Another behavioral peculiarity of high mountain birds is lack of activity in male song. Exposed landscape, low atmospheric pressure, permanent cold winds and poor sound environment are not favorable for singing. Males of many species which normally utter frequent loud nuptial songs at low altitudes sing rarely and quietly in the highlands. Songs, such as those of the black redstart *Phoenicurus ochruros*, larks, accentors and wheatears are audible only for short distances. The same is true for the highland endemics: Güldenstadt's redstart *Phoenicurus erythrogastus*, grandala and Roborowski's rosefinch *Kozlowia roborowskii*. Moreover, other highland birds, such as Brandt's rose-finch, twite and all snowfinch species have no special nuptial song. Of the few exceptions, the most obvious are the snowcocks with their loud nuptial and communicational calls and whistles, which are audible for a kilometer or more.

Scarcity of food sources in the highlands affects

Table 2 Clutch size in some of highland birds (38°N)

Species	Clutch size	
	Lowlands	Highlands
<i>Calandrella acutirostris</i>	4 – 5	3
<i>Eremophila alpestris</i>	4 – 5	1 – 3
<i>Delichon urbica</i>	3 – 7	2 – 3
<i>Riparia rupestris</i>	4 – 5	3 – 4
<i>Pyrhhorcorax pyrrhcorax</i>	3 – 9	3
<i>Cinclus cinclus</i>	4 – 5	1 – 2
<i>Oenanthe deserti</i>	4 – 6	3 – 4
<i>Phoenicurus ochruros</i>	5 – 6	4
<i>Prunella fulvescens</i>	3 – 5	3
<i>Motacilla alba</i>	4 – 5	2
<i>Montifringilla nivalis</i>	4 – 6	4
<i>Tadorna ferruginea</i>	8 – 12	8 – 12
<i>Tringa totanus</i>	3 – 4	3 – 4
<i>Motacilla citreola</i>	4 – 5	4 – 5
<i>Carduelis flavirostris</i>	4 – 5	4 – 5
<i>Bucanetes mongolicus</i>	5	5

reproduction levels in some species, mainly insectivores negatively. Many bird species adapt by decreasing clutch size. In comparison with those in congeners or conspecifics, clutch size is smaller in species and populations breeding at high altitudes (Table 2). This tendency is well pronounced even within endemic highland species. Grandalas possess the minimal clutch size for the Turdidae: 1 – 2 eggs only. Some authors assume that such reductions are the result of specific highland conditions, such as the low atmospheric pressure etc. If so, these factors should be present in all highland species. But it is not so! Where food resources are sufficient, clutch size is much the same as at low altitudes (Potapov, 1966a). For example, such common highland species as the bar-headed goose, ruddy shelduck, all snowcocks, Brandt's rosefinch and most of herbivorous species have clutches of normal size. Even insectivores lay normal clutches where food is abundant, as in the case of species that nest in the more productive marshy sub-alpine meadows (citrine wagtail, common redshank).

The life cycle of Brandt's rosefinch is a good example of adaptation to high mountain conditions. Except during breeding, the rosefinch lives in flocks that feed year-round on grass seeds on mountain slopes, even in winter; they never leave snowless parts of the highlands despite strong night frosts (up to – 45 °C). Effective solar radiation by day, the high nutritional value of seeds and the absence of snow allow them, like some other highland birds, to spend the winter in their breeding areas. They protect themselves from night frosts as well by using a strategy effective for other social birds: they gather in collective roosts in caves or cavities in the rocks, protected from winds, where dozens to hundreds of them spend the night huddled close together. Snowcocks also gather in communal nocturnal roosts, as do some highland birds in the South American Andes (Dorst, 1963).

The breeding period in Brandt's rosefinch is late in the season and closely correlated with the ripening of grasses in sub-alpine and alpine meadows. The first flush of full seeding begins on the floors of highland valleys in early July, and is the signal for the finches to start breeding. They reach these feeding grounds from their breeding zone in the upper alpine belt by the modes of flight described above(3.2). But the question remains: why does the finch nest so far above its feeding grounds? The answer is humidity which is significantly higher there than at lower altitudes. In the Pamir, this breeding zone coincides with the zone of maximal precipitation.

The altitudinal distance between nesting and feeding grounds is maximal at the very beginning of



hatching, and varies from 800 up to 1 000 m. In the course of rearing the young, this distance decreases daily in accord with a progressive rise in the zone of ripening grass seeds. As young approach fledging, when their food consumption becomes maximal, the drop to the zone of ripening grass seeds falls to only about 300 – 400 m, easing the effort of parents returning with food. By late August, when young rosefinches leave the nest, the level of seeding grasses reaches the breeding zone itself. Young Brandt's rosefinches leave their nests, as do young grandalas, later than all other highland birds and, like some young snowcocks, do not have time to mature by the next spring; they start to breed only in their third summer (second year after birth).

The need to transport seeds long distances to young has been the driver for developing an effective morphological adaptation in the rosefinch: two gular sacs under the tongue that can carry nearly 5 g of seeds, enabling parents to feed nestlings no more than once per hour. These sacs are functional only during breeding. Similar pouches are found in other species of rosefinches (*Carpodacus* sp.) and some other mountain finches as well—Mongolian trumpeter and crimson-winged finches *Rhodopechys sanguineus* (Miller, 1941; Potapov, 1963; Kovshar and Nekrasov, 1967; Neufeldt, 1986). Even choughs have an alimentary organ (expanded esophagus) for transporting food to nestlings. During breeding, the upper part of the esophagus expands into a sac with enough space to hold considerable quantities of food.

## 4 Conclusion

The bird life of the Eurasian highlands still remains one of the most poorly studied areas of faunistic ornithology. This is a serious drawback, because, among global biomes, the ecosystems of the highlands are some of the least modified by humans and so valuable controls in investigating of bird-environment interactions. There are still serious gaps of information in many areas of highland bird ecology, such as the altitudinal limits of breeding for many species, their diet, the role of dark pigmentation in the skin of

nestling in relation to ultraviolet radiation, structure of egg shell and its adaptation to arid climate, population dynamics, and time and energy budgets. I hope that this address will generate much more interest in high mountain birds, especially by young ornithologists—because field work in the highlands needs the youthful health and stamina of an ironman.

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## A basal archosaurian origin for birds

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**Abstract** The controversy over the origin of birds may have been resolved through the discovery of new and remarkable fossils from the Triassic of Central Asia and the Early Cretaceous of China. Flight probably originated in small, quadrupedal gliding archosaurs in the Triassic. Feathers originated for gliding rather than for insulation. The “maniraptoran dinosaurs” are actually derived from birds with at least gliding capabilities and primary feathers on the hands [Acta Zoologica Sinica 50 (6): 978–990, 2004].

**Key words** Birds, Origin, Archosaurs, Maniraptorans, Phylogeny

## 鸟类起源于基干的初龙类

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**摘要** 中亚三叠纪和中国早白垩世的新的化石发现或许可以帮助解决有关鸟类起源的争议。鸟类的飞行可能起源于三叠纪一些小型的、四脚滑翔的初龙类。羽毛的起源最初是为了滑翔而不是保温。“手盗龙类”实际上起源于鸟类，并至少发育了初级飞羽，具备滑翔的能力 [动物学报 50 (6): 978–990, 2004]。

**关键词** 鸟类 起源 初龙 手盗龙 系统发育

### 1 Introduction

*Archaeopteryx* was the first bird to be recognized from the Mesozoic and displayed such a remarkable combination of avian and reptilian characters that it became the archetype of a “missing link.” It was discovered in 1861, only two years after publication of Darwin’s *Origin of Species*. Little doubt remains that birds originated from reptiles, but controversy exists over the choice of reptile. Huxley (1870) was an early proponent of dinosaurs as ancestors for birds, and this was the dominant theory of avian origins until the beginning of the 20th Century (Witmer, 1991). The discovery at that time of older bipedal archosaurs provided new models lacking specializations that seemed to bar dinosaurs from direct avian ancestry. Heilmann’s (1926) book “*The Origin of Birds*” related birds to dinosaurs through a basal archosaurian stalk. Almost everybody who read his book agreed with him, and the dinosaur-bird connection was buried for over forty years until exhumed by Ostrom (1973), and used to support endothermy in dinosaurs.

The remarkable public attention garnered by dinosaurs at this time contributed to the success of a

theory relating them to birds. Ostrom (1973, 1976) used an essentially man-sized theropod *Deinonychus* as the model for his idea. He met with immediate acceptance among dinosaur paleontologists and resistance in the ornithological community (Feduccia, 1980). For nearly two decades, *Deinonychus* stood almost alone as a dinosaurian proxy for a bird ancestor, but in recent years, smaller and more bird-like theropods were discovered in the Early Cretaceous *Confuciusornis* fauna of Liaoning, China. Some of the new fossils preserve soft parts including feathers. These deposits are nearly twenty million years younger than *Archaeopteryx* (1 200 000 years old or a little older). While these deposits are much younger than the time of the origin of birds, the diversity and quality of pertinent fossils make them critical to our understanding of how birds may have originated.

### 2 Avian flight

The origin of avian flight is intertwined with the origin of birds. Pterosaurs and bats incorporate arms and legs into a continuous patagium and can be compared directly with living examples of gliding mammals; but in birds, the legs and wings are decoupled

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with little evidence that an extensive skin patagium was ever present. Birds are accomplished bipeds, while bats and pterosaurs are basically quadrupedal. If avian flight originated in an arboreal environment, should bipedality be an expected precursor as some have suggested (Ostrom, 1979)? Were hand movements involved with capturing prey in small bipedal dinosaurs modified to supplement the thrust of the legs in running (Gishlick, 2001) and, with further modification, led to flight from the “ground-up”? Because the airfoil surface in birds is composed of feathers, this scenario presupposes that feathers had already evolved. Most supporters of a cursorial origin for flight assume that feathers originated for a function unrelated to flight (insulation, prey capture) and were later recruited for aerial propulsion. (Ostrom, 1979).

Many dinosaurs were bipedal runners balancing a teetering body on their hind legs. The back was held horizontal and the stride was exceptionally long for the length of the body (Jones, et al., 2000a). This long stride may have been the secret of dinosaurian success for nearly 180 000 000 years. Anatomical features associated with this posture—reduced forelimbs attached to a posteroventral glenoid and open acetabulum with a supra-acetabular shelf—are among the important characters defining Dinosauria (Benton, 1990). The hind legs were elongated and the feet digitigrade. The body cavity in most dinosaurs was deep and laterally compressed. Few researchers see a climber in these proportions, and proponents of a dinosaurian origin of birds mostly thought that flight originated in small bipedal dinosaurs which achieved flight speed through running (Williston, 1879; Padian, 1985). The opposing view that flight originated in small arboreal reptiles came from Williston’s former mentor, O. C. Marsh of Yale (Marsh, 1880). Both ideas have strengths and weaknesses. Small running animals lack the stride length necessary to achieve useful speeds (Rayner, 1985). The original feathers created drag slowing their bearers down, and made little adaptive sense for animals that already had too much drag and too little airspeed. Animals jumping out of trees had the opposite problem: too much airspeed and too little drag. Feathers should work for them immediately, but how were arm movements decoupled from those of the legs?

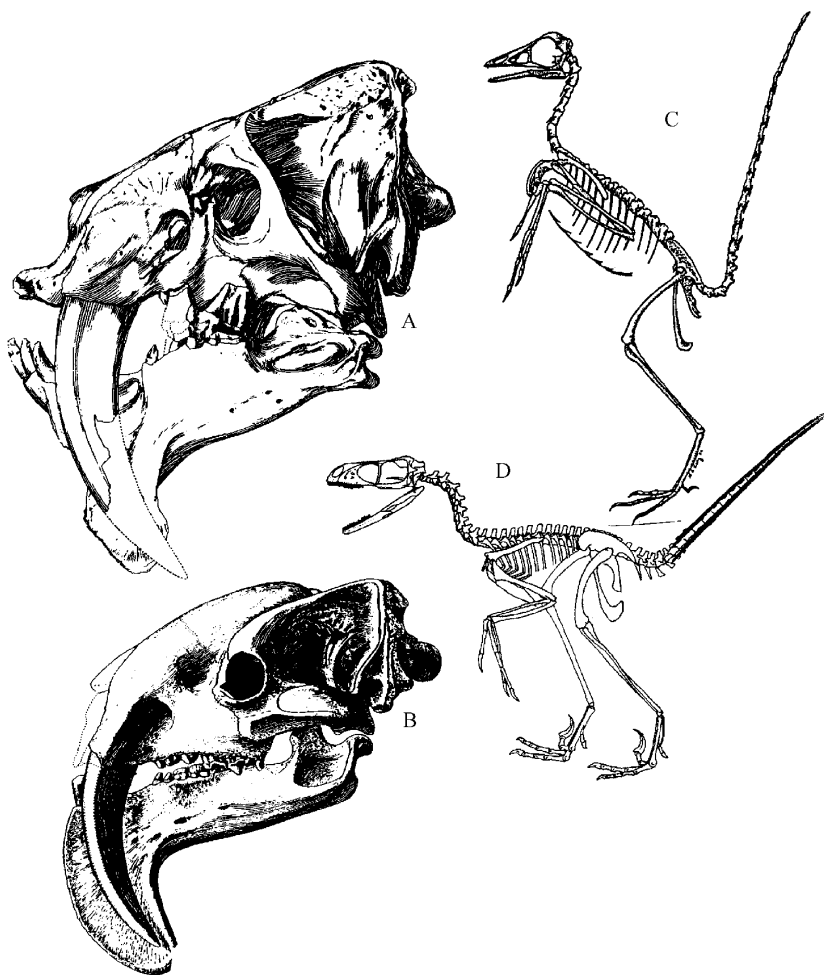
One of the most surprising features of the anatomy of *Archaeopteryx* is its poorly developed parasagittal posture. The femoral head turns forwards rather than extending perpendicular to the shaft. The pelvis has an incompletely open acetabulum, and there is no characteristic dinosaurian supra-acetabular shelf (Martin, 1991, Figs. 30–31, 34, 38–42). This results in a somewhat sprawling position for the

femur (Martin, 1991, Fig. 37) that is corrected at the knee joint, resulting in a functionally vertical leg. Modern birds have an antitrochanter on the acetabulum producing a similar divergence of the femora. This positioning permits modern birds to extend the femora forwards on either side of a broad ribcage. Their sprawl is also corrected at the knee. *Archaeopteryx* lacks basic features of both modern bird and dinosaur postures; and it is difficult to argue that it shared their peculiar backs when running, or that the common ancestor of birds and dinosaurs had already achieved such a running posture. In fact, confinement of the articular surface to the front of the acetabulum in *Archaeopteryx* results in a vertical back (Fig. 1). This posture raises the wing further from the ground permitting a more complete wing beat, a position assumed by modern birds at the point of take-off from the ground. *Archaeopteryx* appears to have been a poor runner when compared to contemporary dinosaurs. Recent analysis of phalangeal proportions (Hopson, 2001; Zhou and Farlow, 2001) shows adaptation for terrestrial locomotion at about the level of a pigeon.

Bergers and Chiappe (1999) attempted to bolster the cursorial model by proposing that power exerted by the legs could be supplemented with wing thrust. Because the wings would have to pull the animal faster than it could run, it is difficult to understand how this could work, particularly as running birds usually have small wings that are held against the body to reduce drag rather than flapped. Dial (2003) offered evidence for wing-assisted vertical running where the wing beat permits the climbing of near vertical surfaces by keeping the animal pressed to the surface rather than providing lift. This might actually provide a special case for the arboreal model where the protobird could spend time on the ground, and still run up a tree to achieve altitude for takeoff. Dial’s description seems better fitted for modern birds with their peculiar leg positioning than *Archaeopteryx*, and incompatible with the Bergers and Chiappe (1999) model. There is a strong probability that bipedal locomotion is secondary to flight in birds, and that the avian ancestor was an arboreal quadrupedal glider.

### 3 Dinosaurian origin of birds

No one doubts that some Cretaceous dinosaurs are remarkably similar to certain fossil birds. The question remains: how much of this similarity can be ascribed to convergent evolution and how much to direct relationship. To evaluate this question, let us compare the very bird-like maniraptoran *Bambiraptor feinbergi* with the primitive bird *Archaeopteryx* (Fig. 1: C, D). We see pronounced similarity, but



**Fig.1 Convergence versus homology**

Skull and jaws of the placental saber-tooth *Barbourofelis*. (A) compared to the very distantly related marsupial saber-tooth *Thylacosmilus* (B) Is the skeleton of the early bird *Archaeopteryx* (C) more similar to that of the birdlike “dinosaur” *Bambiraptor* (D) than the convergent saber-tooths are to one another? (A–B from Martin, 1994; Fig.7)

is it greater than that between the nimravid saber-tooth *Barbourofelis*, and the saber-toothed marsupial *Thylacosmilus* (Fig.1: A, B). These two mammals are about as distant phylogenetically as anyone has suggested for birds and dinosaurs, yet they share an extensive list of apomorphic (derived) characters. Clearly, convergence is powerful enough to confound an insufficiently critical phylogenetic analysis. A careful study of structural detail yields evidence that the saber tooth similarities were derived independently, and nobody thinks that there is an exclusive phylogenetic relationship between marsupial and placental saber-tooths. We should require a similarly rigorous study of structural detail before we accept a dinosaurian origin of birds. In particular, we should be able to offer some explanation for a “temporal paradox” and certain “anatomical barricades” that I will now address.

#### 4 The temporal paradox

In most phylogenetic analyses (e.g., Sereno,

1999), birds are not simply closely related to dinosaurs but are actually members of the maniraptorans, the last dinosaurian clade to develop (i.e., a crown-group). Because birds are embedded within the maniraptorans, they can be regarded as living dinosaurs (Dingus and Rowe, 1998). All other major clades of saurischian dinosaurs precede the origin of birds. This creates an inconsistency in time of origin for *Protoavis*, a supposed Late Triassic bird (Chatterjee, 1995); and a similar problem exists for possible Early Jurassic “bird” tracks (Lockley et al., 1992). Even if *Protoavis* were only a dinosaur closely related to birds, all dinosaur clades preceding it must have been in existence, along with their signature characteristics, by the Late Triassic. Almost all of dinosaur evolution would have occurred in a sudden burst at about the time that dinosaurs first appear in the fossil record.

Embedding birds in the maniraptoran crown group coupled with a Late Jurassic age for *Archaeopteryx* creates a similar problem. Not only is

*Archaeopteryx* older than any creditable maniraptoran fossil (Feduccia, 2002), but maniraptoran diversification must be even older. This results in a hypothetical burst of evolutionary diversification in the Middle Jurassic (Sereni, 1999). Such discrete evolutionary bursts, if genuine, are more theoretically important than the question of avian origins and should be tested with evidence outside the bird/dinosaur controversy. They may also be a warning of some flaw in the cladistic analysis.

The opposing view is well articulated in the *Origin and Evolution of Birds* by Feduccia (1999). This book argues that birds are very ancient, extending into the Triassic, well before the appearance of the first dinosaurs. The ancestors of birds were cold-blooded, small and lizard-like. They lived in trees, and feathers probably evolved for flight and only later as insulation. Flight evolved from jumping from tree to tree; landing on the ground was initially an unhappy accident ('trees-down' origin of flight). Bipedality was a consequence of their arboreal lifestyle, as has been suggested for primates (Martin, 1983a, b, 1987); and the elongated foot resulted from jumping rather than terrestrial running. The 'trees-down' theory has the additional advantage of having living models for postulated evolutionary stages leading to flight (Bock, 1965, 1985).

## 5 Anatomical barricades

If dinosaurs are to be considered avian ancestors, several anatomical problems need to be resolved. The most serious concern the teeth and the hand. The nature of tooth implantation and replacement is critical (Wellnhofer, 1974; Martin and Stewart, 1999). These are fundamental features, and once one implantation pattern has been achieved, it is hard to understand why it would be lost and replaced by another. In birds and living crocodilians, teeth are originally implanted in a groove with sockets forming around the roots from front to back as the jaw matures. There is not enough space for the lingual tooth family, and a replacement tooth quickly migrates under the crown of its predecessor. It then finishes its development and ascends vertically. Crocodilians may show several replacement teeth stacked vertically and vertical tooth replacement is known in *Archaeopteryx* and other toothed birds (Martin and Stewart, 1999; Martin and Zhou, 1997).

Dinosaurs retain a primitive pattern of tooth replacement in which the young teeth are arranged horizontally in a lingual row. The teeth in birds or crocodiles are bordered lingually by an extension of the tooth bearing bone (premaxilla; maxilla or dentary), while dinosaur teeth are bordered by hypertrophied attachment bone (superpleurodonty; Martin

and Stewart, 1999). This suggests that the common ancestor of birds and dinosaurs did not have socketted teeth. The teeth of birds are uniform in having a short crown with a constriction near the base leading into an expanded root that usually includes an oval replacement pit. Similar teeth have not been described in dinosaurs, although dromaeosaurs were originally reported to lack interdental plates, a signature trait of dinosaurian tooth implantation. Their tooth replacement has also been claimed to be bird-like (Currie, 1987). If they had, or had had, the avian/crocodilian implantation and replacement pattern, we might argue instead that they are not dinosaurs. The common ancestor for both birds and dinosaurs would pre-date thecodonty in either group and lie at the base of the Archosaurian radiation.

Much of Ostrom's original evidence for a bird/dinosaur relationship was based on the wrist and hand. Wrists in the advanced maniraptorans, *Velociraptor* and *Bambiraptor*, show only two free bones, as reported by Ostrom (1969) for *Deinonychus*; but the semilunate is in the distal row as in birds (Padian and Chiappe 1998a, b) and not a proximal carpal (radiale) as reported by Ostrom (1969). In birds, the equivalent should be a distal carpal III, and this condition seems clear in *Jeholornis* and *Confuciusornis* from the Early Cretaceous of China where it only fuses to metacarpal III. In dinosaurs it should be fused distal carpals I, II. The small distal carpal IV found in birds is lost; and there is presently no evidence that the small distal carpal identified in *Deinonychus* by Padian and Chiappe (1998a, b) is distal carpal IV. There is a single proximal carpal, the radiale (ulnare of Ostrom, 1969). The metacarpals are arranged in an arch as restored by Ostrom, different from that in birds. The wrist in *Archaeopteryx* and modern birds is less derived in these respects, making maniraptorans more likely the descendants of birds than their ancestors.

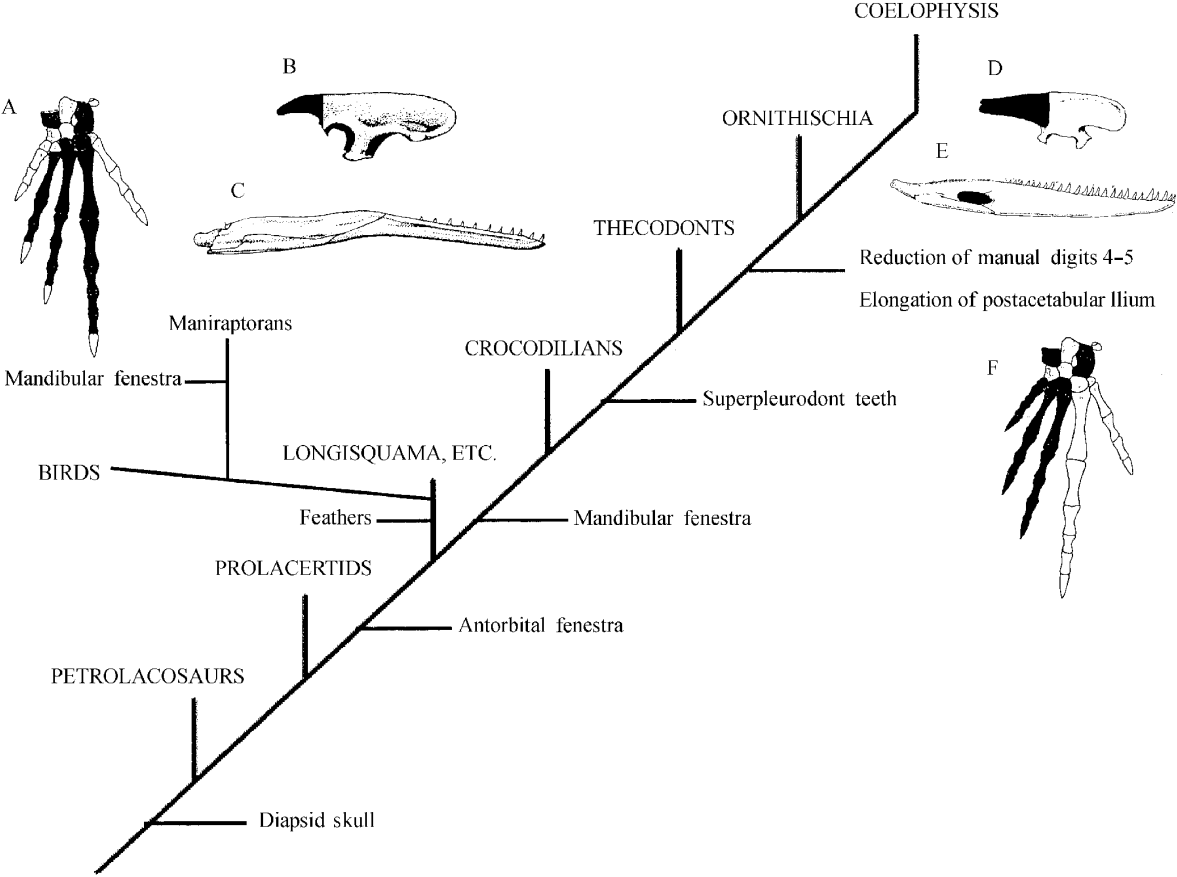
The pattern of finger reduction in dinosaurs is unique and might be the best evidence for the monophyly of the group. In most other tetrapods, digit reduction proceeds from both sides inwards (perrisodactyls and artiodactyls). In dinosaurs, digit reduction is restricted to the lateral side of the hand with digits 4 – 5 reduced in the Triassic dinosaur, prosauropods and ornithischians (Feduccia, 2002). Birds clearly retain digits 2 – 4, as shown by embryological development of a five-digit hand in the ostrich (Feduccia and Nowicki, 2002) and work by Larsson and Wagner (2002) using molecular markers to identify digit condensations in the chicken embryo. As pointed out by Ostrom (1985), there are no direct data available for the pattern of digit reduction in dromaeosaurs, but an avian pattern would provide addi-

tional evidence that they are not dinosaurs. The common ancestor of advanced maniraptorans such as *Bambiraptor* and modern birds had not yet lost the ulnare or distal carpal IV. The common ancestor of birds and maniraptorians on a dinosaurian lineage must precede Triassic dinosaurs that already show the reduction of digit 4 (Fig.2).

Ostrom (1969) figured the proximal ankle (astragalus and calcaneum) of *Archaeopteryx* in several drawings and two photographs that compare the ascending process in the ankle to that of *Deinonychus*. This was one of Huxley's (1870) original features associating dinosaurs and birds, but the ascending process in birds (Martin et al., 1980) is a separate "pretibial bone." The pretibial bone is more closely united with the calcaneum than with the astragalus in most modern birds and extends up the lateral rather than medial side of the tibia. Ostrom's excellent photographs (Ostrom, 1976) clearly show that in *Archaeopteryx*, it is also a long narrow process on the

lateral side of the tibia, lying above the calcaneum and along the fibula. In the London specimen it pulled off with the calcaneum and remains on the counter slab. This position is the same as in most other birds and differs from dinosaurs.

In a *lapsus*, Ostrom (1976, Fig.29) reversed the position of the ascending process, thus making the restoration more comparable to *Deinonychus*. This error was pointed out by Martin (1983a) and Tarsitano and Hecht (1980). It was corrected by Ostrom (1985, p. 174): "I further admit to confusing the issue by illustrating this process in *Archaeopteryx* in my 1976 paper in a much more medial position than it is actually preserved in the London and Berlin specimens". All of Ostrom's illustrations in this paper differ widely from one another (Martin et al., 1980). One (Ostrom, 1976, Fig.28) is essentially identical to the condition in *Deinonychus*, showing a very reduced calcaneum and a broad ascending process from the astragalus. In fact, *Archaeopteryx* more



**Fig.2** Diapsid reptiles and birds showing the point of first occurrence of various synapomorphies

The pattern of finger reduction (A, F) is illustrated by the hand of *Petrolacosaurus* (Reiz, 1981). A: Shaded wrist and digits preserved in birds and presumably maniraptorans. F: Those preserved in dinosaurs. The absence of the mandibular fenestra in early birds is illustrated by *Archaeopteryx* (C); it presumably would be a neomorph in maniraptorans. It is primitively present in dinosaurs, including *Coelophysis* (E, based on Colbert, 1974). The primitively short postacetabular ilium (shaded) is illustrated by *Archaeopteryx* (B) and contrasted with *Coelophysis* (D) (from Naples et al., 2002). The pattern of avian primitive structures supports a very early divergence from the line leading to dinosaurs. If maniraptorans are actually birds, their divergence would be equally early and their resemblance to dinosaurs convergent.

closely resembles carinates than ratites in this region, and is also similar to primitive ornithurines such as *Baptornis* and *Hesperornis*. In these birds, the calcaneum is large and forms the outer condyle as is usual in reptiles. In some early birds (enantiornithines) and many dinosaurs, the astragalus enlarges and the calcaneum becomes vestigial, clearly a more derived condition. We can speculate that the common ancestor of birds and dinosaurs lacked an ascending process on the ankle, and that bipedality was achieved independently.

Additional avian features that are primitive when compared to dinosaurs in general include a short post-acetabular ilium (Naples et al., 2002). The post-acetabular ilium is already elongated in the coelurosaurian dinosaur *Coelophysis* from the Triassic (Fig. 2). The absence of a mandibular fenestra in most Mesozoic birds, a condition already present in late Triassic archosaurs, including crocodylians and dinosaurs, indicates also that the basal avian stalk appeared close to the origin of archosaurs, a position consistent with evidence from tooth implantation (Fig. 2). The independent evolution of an ascending process in the ankle (pre-tibial bone in birds; ascending process of the astragalus in dinosaurs) indicates that their common ancestor predates the characteristic hind-leg posture of dinosaurs; and this is further indicated by the slightly sprawling hind-leg of *Archaeopteryx*, accompanied by partial closure of the acetabulum (Martin, 1991).

The demonstration that these features are constructed differently in dinosaurs and birds is not simply a criticism of their use in relating dinosaurs to birds. Rather we may also suppose that their common ancestor had not yet solved these particular problems. We may then go to the cladogram and constrain the point of appearance of the common ancestor (Fig. 2). The distinctly different patterns of tooth replacement and implantation, absence of a mandibular fenestra, pattern of finger reduction, short post-acetabular ilium and presence of a pre-tibial bone point clearly to a common bird/dinosaur ancestor preceding the triassic coelurosaurs *Coelophysis*, *Syntarsus*. If maniraptorians share a special ancestor with birds, it must also lie below certain cladistic points (serrated teeth, mandibular fenestrae, ossified sternum, reduced wrists, erect femora, enlarged pedal II claw and tail rods). *Archaeopteryx* has a few derived features, including a slightly shortened tail, which suggest that it is not the ancestor of maniraptorans; but any common ancestor of maniraptorans and birds looked more like it than like *Coelophysis*.

## 6 Feathered dinosaurs?

The origin of birds is closely coupled with the origin of feathers and related skin features. The inter-

vention of a network of skin muscles (Homberger, 2002) that can distort the follicle and thereby move the feather is such a significant part of their functional morphology that we may suppose that the evolution of feathers and the muscles that moved them was closely correlated. As soon as feathers achieved sufficient length to form a useful airfoil, they needed a mechanism to fold them out of the way. This folding utilized a sideways motion that would be impossible for an ordinary scale. In feathers, however, it is made possible by a pivot point provided by a rod-like calamus inserted deeply within a dermal pocket (follicle). Long flight feathers imply the existence of an adequately broad fold of skin to accommodate a deep follicle. In order to provide an airfoil, the feather must also be broad distally. This combination of narrow proximal and broad distal ends is the signature achievement of a feather and separates it from hair and ordinary scales. The airfoil surface of the feather develops within a tube, the feather sheath, where the barbs are folded. They unfold distally as the sheath falls away, permitting the feather tip to become much wider than the base.

The announcement of feathers in a compsognathid dinosaur *Sinosauropteryx* raised the possibility that feathers were widely distributed among dinosaurs. However, none of the above features of feathers could be confirmed in *Sinosauropteryx*. Similar structures have been found in dromaeosaurs where they are claimed to show evidence of feather structure (Xu et al., 2001) and in a pterosaur (Wang and Zhou, 2002). Such a wide phylogenetic distribution of primitive feathers or hairy coverings seems improbable. Could they be features from under the skin rather than above it e.g., collagen fibers? Fossils of superficial muscle in the marine reptile *Ichthyosaurus* (Lingham-Soliar, 1999), do duplicate many feather-like features.

Undoubted feathers (Xu et al., 2001) occur in some putative dinosaurs, including *Protarchaeopteryx*, *Microraptor* (*Archaeoraptor*?) and *Caudipteryx*. *Protarchaeopteryx* (Ji et al., 1998) has typically avian teeth, and there is no reason to doubt that it is avian. *Caudipteryx* has recently been allied with oviraptors (Sereno, 1999). Several workers have considered it a bird and so have I. The existence of long primary feathers extending from the middle finger of the hand requires a long fold of skin to accommodate the calamus. This so greatly reduces the usefulness of the hand for grasping that it must imply derivation from an arboreal flyer/glider. An arboreal stage is further supported by a reflexed hallux on the foot in all of these forms. The most recent cladistic analyses of oviraptorosaur relationships (Lu et al., 2002; Maryanska et al., 2002) show ovirap-

tosaur as flightless birds more derived than *Archaeopteryx*. We thus have animals that are clearly dinosaurs with structures (protofeathers) that do not seem to be feathers, and animals that clearly have feathers and are also birds with primary feathers on the middle finger of the hand.

The most informative specimens are maniraptorans with obvious flight feathers coming off the arm and the hind leg (Norell et al., 2002; Czerkas et al., 2002). One of these, *Cryptovolans pauli*, (Norell et al., 2002) was described as having a rear wing, but Czerkas et al. (2002) suggested that this was too exceptional to be correctly interpreted. New material assigned to *Microraptor* (Xu et al., 2003) now confirms the existence of a rear wing and shows that the longest of the hind leg flight feathers actually come off of the foot (Fig.3)! I was fortunate to be able to examine that specimen in detail and to study a second specimen without preserved feathers but with an excellent skeleton. I also saw photographs of several other similar specimens. It seems clear that long flight feathers very similar to the primary feathers of the hand came off the *tarsometatarsus*, and that the animal had two sets of wings (Fig.3).

This is a remarkable and unexpected confirmation of the tetrapteryx stage in the origin of avian flight predicted by Beebe (1915). It is clearly a gliding adaptation, with feathers taking the place of the skin patagium found in gliding mammals. The femora are unusually long, and in order for the femur to function they must be able to extend laterally, as is the case in pterosaurs. Modifications of the proximal femur and acetabulum for this position result in an animal that could barely walk, let alone run. It must have been completely arboreal. Also supportive of this interpretation are the remarkably small toes on the foot, coupled with a reflexed hallux. The second pedal claw is enlarged but it seems unlikely that it had a predatory function; it was probably used for climbing. The tail includes stiffening rods extending anteriorly from the prezygopophyses and the chevrons. These two features imply relationship with younger forms such as *Velociraptor* and *Bambiraptor*.

The scapula-coracoid complex in the new "*Microraptor*" is arranged as in birds. There is a furcula and an ossified sternum. The pubes are reflected posteriorly, the number of caudal vertebrae is reduced, the astragalus is enlarged and the calcaneum reduced. In some respects these animals are derived compared to *Archaeopteryx* and in ways that bring them closer to terrestrial maniraptorans. They are also some twenty million years younger than *Archaeopteryx*. It is hard to see how a functional biped could have given rise to such an animal. The evolution of a hind limb wing seems to require a quadrupedal arboreal stage.

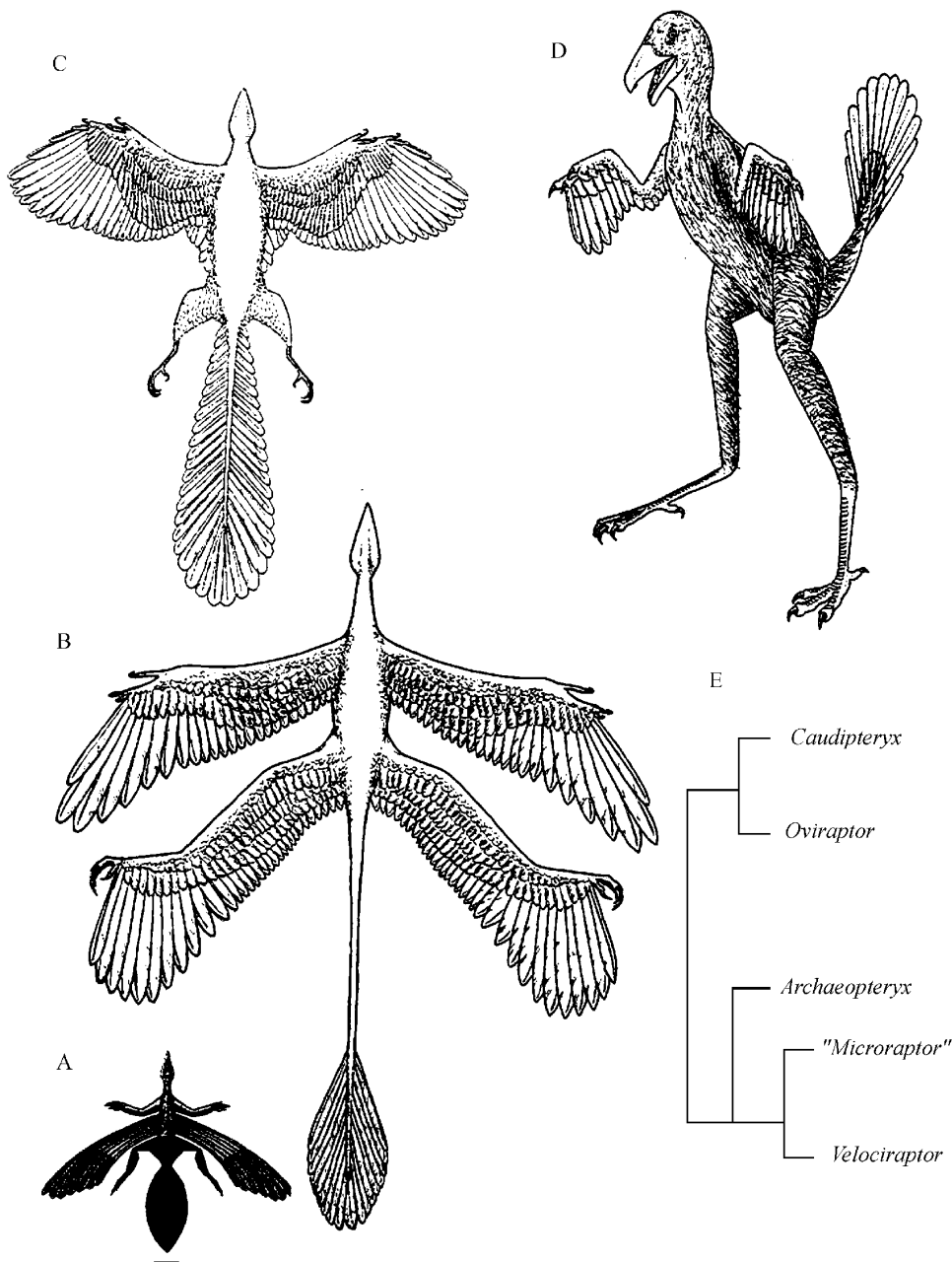
So the late Cretaceous bipedal species must be secondarily flightless, becoming more dinosaur-like than their flying (gliding) progenitors. This is remarkably similar to the pattern of evolution postulated for living ratites, and is a confirmation of the heretical hypothesis of Paul (1984, 2001, 2002). Paul solved the temporal paradox by postulating that *Velociraptor* and other maniraptorans were derived from *Archaeopteryx*-like forms. Paul's hypothesis is supported by the identification of *Microraptor* as a basal dromaeosaur (Xu et al., 2003).

In a recent cladogram (Hwang et al., 2002), oviraptorosaurs including *Caudipteryx*, an animal with genuine primary feathers coming off of the hand indicative of a flying/gliding ancestor, are coupled with a real bird *Archaeopteryx* that lies next to dromaeosaurs including *Microraptor gui*, a flying/gliding form with primary feathers (Fig.3: E)! Can we doubt that the common ancestor of these three taxa also had primary feathers or that their unusual distribution of tail feathers was already present in the common ancestor of oviraptorosaurs and dromaeosaurs? The inclusion of *Archaeopteryx* which lacks this tail structure and a mandibular fenestra seems less likely. The terrestrial maniraptorans might then be thought of as flightless birds. Their ancestor would probably have looked more like an arboreal gliding lizard than a dinosaur.

## 7 Basal archosaurs?

Martin (1983a) discussed *Scleromochlus* as a protobird. Padian (1984) followed von Huhne in allying it with pterosaurs, but Sereno (1991) called it a "dinosauromorph". Apparently it lies at a position near the base of the archosaur radiation and has features suitable for derivation of a flying animal (pterosaur or bird). It seems specialized for jumping, and the weak hand with short fingers would seem to exclude most arboreal activities. I gave *Scleromochlus* special consideration (Martin, 1983a) because it clearly shows the one feature that I suggested as a minimal requirement for a proto-bird. This is a conformation of the shoulder girdle that puts the arm level with the back and provides for a full range of lateral motion, with the center of mass below the arms. This is achieved through a long narrow strap-like scapula lying parallel to the vertebral column. Strap-like scapulae are known in a number of archosaurs including dinosaurs, pterosaurs and birds. However, only birds, some pterosaurs and certain basal archosaurs have scapulae parallel to the vertebral column. This position probably evolved to facilitate arm motion for climbing; in mammals it is found in primates and bats where the scapula differs, being short and broad.



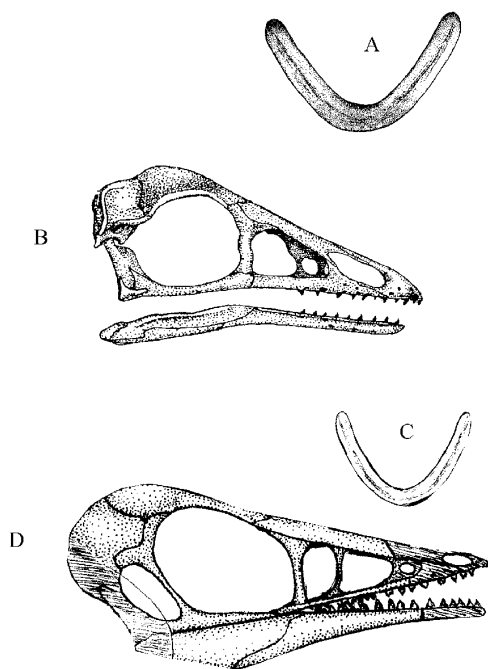


**Fig.3 Various potential stages in avian evolution**  
A. Thoracic wing stage (*Longisquama*): however, tail and hind legs unknown. B. Tetrapteryx stage (*Microraptor*). C. Loss of the rear wing (*Archaeopteryx*). D. Flightless runner (*Caudipteryx*). E. A simplified portion of the Hwang et al. (2002) cladogram showing that forms with primary flight feathers (*Caudipteryx*, *Archaeopteryx*, *Microraptor*) are spread across the cladogram, implying a volant common ancestor.

Long narrow scapulae are also reported for *Longisquama*, *Cosesaurus*, and *Megalancosaurus* (Sharov, 1971; Ellenberger, 1977; Geist and Feduccia, 2000). All of these genera are considered arboreal archosaurs by some authors. Ellenberger (1977) thought that he could detect impressions feathers on *Cosesaurus*. I examined that specimen and could not confirm the presence of feathers, although elongated scales may be present. It clearly has an antorbital fenestra and a furcula. The presence of a furcula seems to be characteristic of these small archosaurs, also oc-

curing in *Longisquama* and *Megalancosaurus*. *Megalancosaurus* was certainly arboreal, as both the front and hind feet show opposable toes; some consider it a glider (Geist and Feduccia, 2000). But the most interesting of this small group of enigmatic animals is *Longisquama* from the Late Triassic of Central Asia. *Longisquama* is represented by a poorly preserved skeleton accompanied by remarkably well-preserved integumentary features described as “nonavian feathers” by Jones et al. (2000b). It has a subdivided antorbital fenestra, pointed snout,

elongate postorbital, teeth with expanded roots (?), elongated strap-like scapula, furcula, elongated penultimate phalanges, and feathers (Fig.4). The cranium is expanded and the neck attaches low on the skull. There is no mandibular fenestra although Sharov (1971) figured a small one. The teeth were described as acrodont (Sharov, 1971), but I think that they are thecodont with a bird-like waisted crown and expanded root (Martin and Stewart, 1999). The hands are very large for the size of the animal. The body is covered with elongated scales, including large flat ones extending from the trailing edge of the arm. The presence of a thoracic wing gives *Longisquama* a distinctly insect-like appearance which has probably discouraged comparison with birds (Figs.5, 6).



**Fig.4** Furcula (A) and skull (B) of *Archaeopteryx* compared to the furcula (C) and skull (D) of *Longisquama*

Initially considered elongated scales by Sharov (hence the name *Longisquama*), and presented as a frill down the back, these structures have undergone drastic reinterpretation. First, Haubold and Buffetaut (1987) correctly recognized that they were arranged in a double row, forming a thoracic “wing” or feather “patagium”. Haubold and Buffetaut are probably wrong in the direction of folding, which actually seems to have been against the back where the “feathers” pivoted on the wide transverse processes of the dorsal vertebrae. But their interpretation of *Longisquama* as an arboreal glider is supported by subsequent investigation. Each vertebral segment has a pair of “feathers”, an arrangement not seen in modern birds but serially homologous with and fundamen-

**Fig.5** Feathers of *Confuciusornis* and *Longisquama*

A: *Confuciusornis* elongated tail feather showing the lower portion in a persistent feather sheath and the distal portion with the feather unfolded. B: Composite *Longisquama* feather showing the calamus, folded barbs within the feather sheath and unfolded sheath with attached rachis and paired barbs. C: Close up showing feather sheath broken away exposing the folded barbs. D: Thoracic wing showing folding pattern.

tally identical to the arrangement of tail feathers in *Archaeopteryx*.

The feather-like structures on *Longisquama* cannot simply be elongated scales, as their tips are twice as wide as the basal portion. Scales are narrower, not wider, at the tip. Feathers have a rounded basal portion that is hollow and contains partitions (pulp caps), all of which can be seen on the structures in *Longisquama* (Jones et al., 2000b). It is almost certain that this region (like the calamus of a feather) was inserted into a follicle. Although we might expect flight feathers to have originated from scales along the edge of supporting structures, they are actually set in, on middle rather than outer fingers in birds and on the midline of the back in *Longisquama*. This type of arrangement would only make sense if they were derived from overlapping scales. Elongated scales often have a central supporting ridge. In the creation of an airfoil, sidebars (barbs) might be added to this ridge. *Longisquama*

**Fig.6** Life reconstructions of *Longisquama* showing both a resting and gliding pose

almost certainly flattened its body when gliding and may have expanded its ribs much as in the prolacer-tian rib gliders. This motion of the ribs would be sim-ilar to that needed to fold and unfold the feathers of *Longisquama*, and rib musculature might have helped with that activity.

Scales are normally incapable of the kind of side-ways motion needed to fold feathers. That the “feathers” of *Longisquama* were capable of this mo-tion is demonstrated by a partially folded wing (Fig. 5). *Longisquama* is like birds too in having integu-mentary structures (Fig.5), where crossbars (barbs) are folded on a rachidal ridge within a tube (the feather sheath). Upon leaving the sheath, the rachis, along with connected barb ridges, unfolds. In modern birds, the rachis and barbs emerge fused to

the sheath (Lucas and Stettenheim, 1972) but quick-ly separate; and as the feather matures, the sheath fragments and falls off. In a mature modern feather, the fabric of the vanes are maintained by an interlock-ing system of barbules and hooklets that is absent from *Longisquama* where the rachis and barbs re-main fused to the unfolded sheath. Barbs towards the tip of the *Longisquama* “feather” occasionally cross over each other, demonstrating local separation of barbs from the sheath near the tip.

Evidence for a feather sheath is an important as-pect of the *Longisquama* fossil. Near the base, its feather has a smooth featureless surface that flakes off to expose underlying folded barbs (Fig.5). On occa-sion these also flake off, revealing a second featureless layer which indicates that the barbs were surrounded.

This is concrete proof that the feather-like structures in *Longisquama* developed within a tube. As feathers are the only integumentary structures known with this kind of development, it is reasonable to interpret these structures as feathers. The only real difference from a modern feather is the persistence of the feather sheath. Fortunately, this primitive condition was retained in the specialized elongated tail feathers found in the Early Cretaceous bird *Confuciusornis sanctis* (Fig. 5). We can thus speculate that *Longisquama* had real feathers of a primitive nature, the essential features of which are present to some degree in unquestioned birds.

Is *Longisquama* a proto-bird? I would not have thought so, but it may be more similar to the prototypic condition than we have supposed. The specialized scales on the trailing edge of the arm clearly have an airfoil structure but seem superfluous when compared to the thoracic wing. Martin (1983a) suggested that powered flight evolved for control of landing location. This may be the function of the arm airfoil, while most of the lift was provided by what amounts to a feather patagium. As the arm airfoil improved, it may have taken over the lift functions of the thoracic wing as the feather patagium shifted to the tail, as in *Archaeopteryx*, until finally lost altogether.

## 8 Conclusions

Gregory Paul's (1984) suggestion that some bird-like dinosaurs are actually secondarily terrestrial birds offers a compromise in a long and heated debate. He gives explanation to relationships that have been expressed in numerous cladograms placing various dinosaurs closer to modern birds than to *Archaeopteryx*. Implicit in such examples is a common ancestor similar to *Archaeopteryx*. Paul suggested (1984, 2001, 2002) that the common ancestor of maniraptorans and modern birds resembled *Archaeopteryx*, thereby solving the problem of the antiquity of *Archaeopteryx* with respect to the mostly Cretaceous maniraptoran radiation, and of numerous anatomical anomalies indicating that these special dinosaurs are too derived to be the ancestors of birds. He also provides an explanation for numerous similarities between maniraptorans and birds. In his model, flight is lost in several lineages and *Deinonychus* can be thought of as a sort of flightless bird! Most of the anatomical changes in this scenario can be duplicated in the evolution of flightless birds such as *Gastornis* from flying ancestors.

A recent study describing oviraptorosaurs as flightless birds (Maryanska et al., 2002), which is based on a detailed and sophisticated cladistic analysis, seems to epitomize the Paulian idea of avian origins. With the discovery of the new four-winged specimens

(e.g., *Cryptovolans*, *Microraptor*), I see little recourse but to accept Paul's general model. The thoracic wing of *Longisquama* and the tetrapteryx theory of Beebe both incorporate a sort of feather patagium analogous to the patagia of flying squirrels and rib-gliding reptiles, placing the origin of avian flight in the main line of gliding adaptation, much as described for it by Bock (1965, 1985).

The maniraptorans are not dinosaurs in this scheme, and their similarity to carnosaurs results from a combination of primitive character retention and parallism. The monophyly of the Dinosauria has always been difficult to support. The peculiar reduction of the outer digits of the hand may be their most significant unifying feature, but it does not include birds and will not include maniraptorans if they are derived from birds.

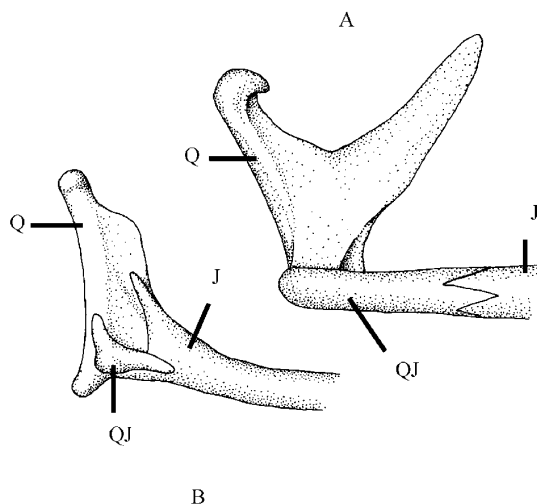


Fig. 7 Quadrate (Q), quadratojugal (QJ) and jugal (J) of the primitive ornithurine *Hesperornis* (A) compared to the sauriurine *Archaeopteryx* (B)

So we may postulate a new scheme for the early evolution of birds as follows:

1) Birds are not the youngest clade of archosaurs, but are one of the oldest, having split off before the development of a mandibular fenestra and socketed teeth.

2) The progenitors of birds were small lizard-like arboreal quadrupeds with elongated scapulae positioned on the back parallel to the vertebral column. They had furculae and elongated scales on their bodies. Bipedality evolved after flight, not before it.

3) Feathers originated for flight, and may have originally been expressed in a thoracic wing as presented in *Longisquama*. The wing on the arm originally developed to control landing and later to extend the flight path. Eventually it was able to take over flight function entirely in some lineages; but in others flight does not appear to have progressed beyond what

might be thought of as powered gliding.

4) Birds went through a tetrapteryx gliding stage; and bipedality probably evolved independently in various lineages.

5) There was a major radiation of birds in the Late Triassic or more probably the Early Jurassic. Birds divided into two fundamental lineages. One of these, the Ornithurae, gave rise to modern birds and modernized the flight apparatus at an early stage (Martin, 1983b, 1987, 1995); ornithurines with essentially modern postcranial skeletons occur in the same beds as *Microraptor* and *Confuciusornis*. Ornithurines all have rod-like quadratojugals (Fig.7).

6) The other half of the avian radiation, the Sauriurae, became extinct with the dinosaurs that they resembled. During the Jurassic, they split into several lineages including *Archaeopteryx* and the enantiornithines (Martin and Zhou, 1997). This clade is usually embedded within the maniraptorans (Fig.4), but maniraptorans may form a more exclusive clade united by the mandibular fenestra and fan-like tail feathers terminating on an elongated tail. Sauriurines all have reduced "L" shaped quadratojugals (Fig.7). Birds that may distribute with specific maniraptorans include *Confuciusornis* with *Caudipteryx* and the oviraptorosaurs. *Jeholornis* seems closer to *Microraptor* and the velociraptorines.

We thus have a surprising conclusion to our debate. The cladograms were correct in embedding some putative dinosaurs within birds, but were incorrect in their relationship to the dinosaur radiation as a whole. We can see this expressed in a recent cladogram (Hwang et al., 2002) relating *Caudipteryx*, *Archaeopteryx* and *Microraptor*. The common ancestor of such a grouping must have looked like a bird and lacked most salient dinosaurian features.

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## Birds as dinosaurs

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**Abstract** The “great debate” over bird origins may never have transpired had the now-famous furcula-bearing, feathered dinosaurs from Asia surfaced when the beds in which they were interred were first discovered in the 1920s. Compelling fossil evidence is now to hand that places birds as a specialized clade within theropod dinosaurs. Major insights include a more seamless fossil record linking birds and non-avian dinosaurs, clear evidence of an early pre-avian origin for feathers and other features previously known only among birds, together with an underscoring of the importance of miniaturization for the evolution of powered flight and a broadening of the functional scenarios for how powered bird flight was first achieved [*Acta Zoologica Sinica* 50 (6): 991–1001, 2004].

**Key words** Dinosaurs, Birds, Flight, *Archaeopteryx*, Evolution

## 被视为恐龙的鸟

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**摘要** 尽管于 20 世纪 20 年代在亚洲地表层首次发现长有羽毛的恐龙和著名的“龙骨突位点”，关于鸟类起源的争论仍没有休止。来自化石的证据表明，鸟类在进化分支上应归于兽脚类的特殊分支。本文主要阐明完好无损的化石揭示的鸟和非鸟类恐龙的亲密关系和鸟类羽毛及鸟类出现以前的羽毛的起源证据，分析体型缩小对飞行进化的重要意义及从新的角度论述鸟类如何飞上了天 [*动物学报* 50 (6): 991–1001, 2004]。

**关键词** 恐龙 鸟 飞行 始祖鸟 进化

## 1 Introduction

### 1.1 Grabau's grab-bag

“These fish are often so numerous that a slab about one foot square will show from 50 to 100 individuals,” remarked Grabau in his 1928 summary of the Early Cretaceous “Jehol fauna” of northern China (p. 672). A sequence of lakebed deposits more than a thousand meters in thickness had been discovered that was literally packed with the remains of the teleost *Lycoptera*, soft-bodied invertebrates and plants (Figs. 1, 2). Now divided into two formations (Yixian and overlying Jiufotang) in Liaoning Province and adjacent areas of Inner Mongolia, the “Jehol Biota” is of world renown for the feathered dinosaurs and primitive birds that came to light during the 1990s (Chen and Fan, 1999; Chang et al., 2003; Zhou et al., 2003).

What if a feathered dinosaur had come to light in

Grabau's time? Less than a day's drive north of Beijing today, this easily accessible outcrop would surely have witnessed the same accelerated exploration that followed the first sensational finds in the 1990s. Most likely, several feathered dinosaurs and toothed birds would have been uncovered by 1925—about the time that Heilmann was finishing his influential treatise concluding that birds were not descendants of dinosaurs (Heilmann, 1926).

### 1.2 Heilmann's hurdle

The crux of Heilmann's argument against dinosaurian affinity involved the lack of any trace of ossified clavicles among dinosaurs then known, and the presence of co-ossified clavicles—a furcula—in *Archaeopteryx* and nearly all other birds (Witmer, 1991). For Heilmann, re-ossification of the clavicles posed an insurmountable evolutionary reversal.

Today, ossified clavicles in the form of a median furcula have been documented in most major non-a-

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**Fig.1 Alternating layers of lake mud and volcanic ash compose much of the Yixian and Jiufotang Formations in western Liaoning Province and eastern Inner Mongolia that have yielded hundreds of well-preserved vertebrates, invertebrates and plants**

Splitting layers by hand is typical of quarry operations like this one in the Jiufotang Formation in southeastern Inner Mongolia (near Nincheng, People's Republic of China).

vian theropod clades, including coelophysoids (Tykoski et al., 2002), spinosaurids (Lipkin and Sereno, in press), allosaurids (Chure and Madsen, 1996), therizinosaurids (Xu et al., 1999a; Zhang et al., 2001), tyrannosaurids (Makovicky and Currie, 1998; Lipkin and Sereno, in press), oviraptorosaurs (Clark et al., 1999; Zhou et al., 2000; Lü, 2002), and dromaeosaurids (Norell et al., 1997; Xu et al., 1999b; Burnham et al., 2000). The furcula, moreover, is preserved in several theropods (*Beipiaosaurus*, *Caudipteryx*, *Sinornithosaurus*) from the “Jehol fauna” in Liaoning (Xu et al., 1999a, b; Zhou et al., 2000; Xu et al., 1999b), and in two further theropods (*Oviraptor*, *Velociraptor*) from the Mongolia, the latter originally named on less complete specimens discovered in the early 1920's (Norell et al., 1997; Clark et al., 1999).

Had any of these specimens come to light when these localities were first explored, Hielmann's sole impediment to a link between dinosaurs and birds would have vanished. Furthermore, several of the

**Fig.2 Hand-dug quarries like this one in the Jiufotang Formation dot the landscape in southeastern Inner Mongolia (near Nincheng, People's Republic of China)**

Dug by local farmers a few years ago, this quarry descends vertically approximately 10 m and then ramifies within the most productive fossil-bearing level.

furcula-bearing Liaoning theropods (*Caudipteryx*, *Sinornithosaurus*, *Microaptor*) also preserve shafted feathers with traces of barbs in a herring-bone arrangement (see below). With dinosaurian furculae and feathers in hand by the close of the 1920's, would the modern “great debate” about bird origins ever have transpired?

### 1.2 “Great debate” or just bad timing?

As it happened, paleontologists would wait nearly a half-century before recovering enough fossil material to piece together the first skeleton of a maniraptoran theropod close to the origin of birds — *Deinonychus* (Ostrom, 1969). Ostrom and *Deinonychus* — without the benefit of dinosaurian furculae or feathers — rekindled Huxley's hypotheses of 1868 (also Williston, 1879) linking *Archaeopteryx* and later birds to the then recently discovered small coelurosaurian *Compsognathus*. Ostrom's papers on bird origins (Ostrom, 1973, 1976a, b) also precipitated the modern “great debate,” just as cladistic methodology was being adopted by a growing number of students in both paleontology and ornithology. During the



decade of the 1980's alone, the number of papers on bird origins exceeds the total on this subject in the preceding century (Witmer, 1991), with two opposed camps emerging: proponents of an archosaur/crocodylomorph origin (e.g., Walker, 1972; Martin, 1983; Feduccia and Wild, 1993; Jones et al., 2001; Feduccia, 2002; Olson, 2002), and those for a theropod origin (e.g., Gauthier, 1986; Holtz, 1994; Sereno, 1997, 1999; Forster et al., 1998; Padian and Chiappe, 1998; Xu et al., 1999b; Norell et al., 2001).

Witmer (2002) documented well the recent history and intensity of the debate, which he attributed to the contrasting inferences to be drawn about non-osteological features (physiology, feathers, flight), depending upon where one roots the class Aves. These issues, however, are surely better understood as manifestations of fundamental methodological differences and collegial allegiances. The most active members of the two principal camps of the debate (archosaur/crocodylomorph vs dinosaur) almost always employ mutually exclusive *phylogenetic methods* (traditional vs cladistic), and typically ally themselves with different *scientific communities* (avian vs dinosaurian paleontology). The fundamental motor of the debate is the clash between methodologies and subdisciplines.

This is well demonstrated in a pair of recent commentaries from traditional paleo-ornithologists in a journal devoted to avian biology (*The Auk*). One (Olson, 2002) was a review of a volume on bird origins in honor of John Ostrom (Gauthier and Gall, 2001), and the other (Feduccia, 2002) a response to Prum's (2002) fact-filled perspective on the accumulating phylogenetic, developmental, and reproductive evidence for the dinosaurian origin of birds. The dramatic new data bearing on the debate (summarized below) has had negligible effect on the small cadre of paleobiologists staunchly opposed to birds as derived theropods, as well as characters and parsimony as the arbiter of homology and relationships (e.g., Feduccia, 1999; Dodson, 2000). Now this opposition has seized upon incontrovertibly-feathered dromaeosaurids, like *Sinornithosaurus*, interpreting them as flightless birds after decades of denigrating Ostrom's structurally identical cousin *Deinonychus* as anything remotely resembling a bird.

The purpose of this paper is not to review such arguments; detailed reviews are available elsewhere (Padian and Chiappe, 1998; Sumida and Brochu, 2000; Prum, 2002, 2003). Under the rapidly increasing weight of evidence today, the "great debate" is fast becoming a historical footnote on the road to understanding the origins of birds, begging the question: if dinosaurian furculae and feathers were in hand

by the close of the 1920's, and a dinosaurian origin accepted then by Hielmann, traditional systematists and paleo-ornithologists, would today's "great debate" ever have transpired?

## 2 Observational evidence

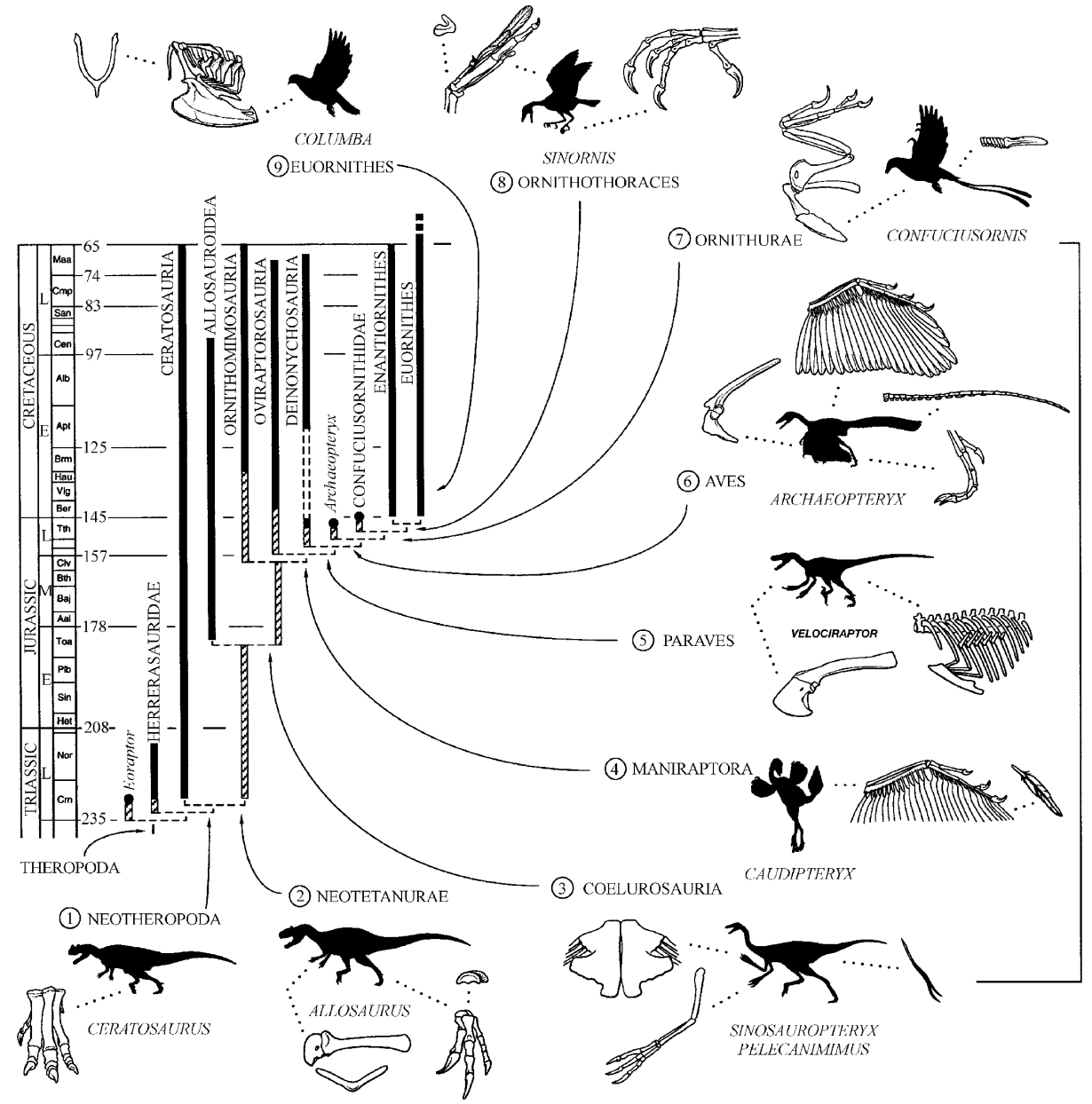
### 2.1 Birdlike dinosaurs

A trove of "birdlike" dinosaurs (here meaning "basal maniraptorans") has been found in the last decade in Cretaceous rocks in Asia and North America. The most spectacular specimens include evidence of the integument and were discovered in a thick lakebed sequence in Liaoning and Inner Mongolia in China, dated radiometrically to the Early Cretaceous (ca. 130 – 110 MYA; Zhou et al., 2003). These include several basal maniraptorans such as the oviraptorosaurian *Caudipteryx* (Ji et al., 1998; Zhou et al., 2000), the troodontid *Sinovenator* (Xu et al., 2002), and the dromaeosaurids *Sinornithosaurus* (Xu et al., 1999b; Xu and Wu, 2001) and *Micro-raptor* (Hwang et al., 2002; Xu et al., 2003). Elsewhere in Asia and North America, dune and fluvial deposits have yielded nearly complete skeletons of dromaeosaurids (Fig. 4) and oviraptorids, filling in nearly all aspects of their osteology (*Velociraptor*: Barsbold and Osmólska, 1999; Norell and Makovicky, 1997, 1999; *Bambiraptor*: Burnham et al., 2000; *Oviraptor*: Clark et al., 1999).

Especially birdlike skeletal characters are revealed in the presence of uncinat processes, furculae, elongate sternal plates buttressed by squared coracoids, and elongate forelimbs with rotary wrist joints (Fig. 3). There are scores of other modifications in virtually all parts of the skeleton that establish a close relationship between non-avian theropods and birds (Sereno, 1999).

### 2.2 Ancient avians

The long-standing gap in the fossil record between *Archaeopteryx* and the toothed birds of the Late Cretaceous, *Ichthyornis* and the hesperornithiforms (Marsh, 1880; Martin, 1980), has now been filled with a series of basal avians slightly larger than *Archaeopteryx* in body size. Those closest to *Archaeopteryx* include *Jeholornis* from Liaoning (Zhou and Zhang, 2002a) and *Rahonavis* from Madagascar (Forster et al., 1998), both of which retain a long bony tail with moderately elongated prezygapophyses and chevrons like *Archaeopteryx* (Fig. 5). *Sapeornis*, also from Liaoning (Zhou and Zhang, 2002b), is more advanced than *Jeholornis* and *Rahonavis*, as evidenced by its shortened caudal series and terminal pygostyle. More advanced than the aforementioned avians is *Confuciusornis*, which exhibits functionally significant modifications of the wing bones and a well developed pygostyle (Hou et al., 1995, 1996) (Fig.



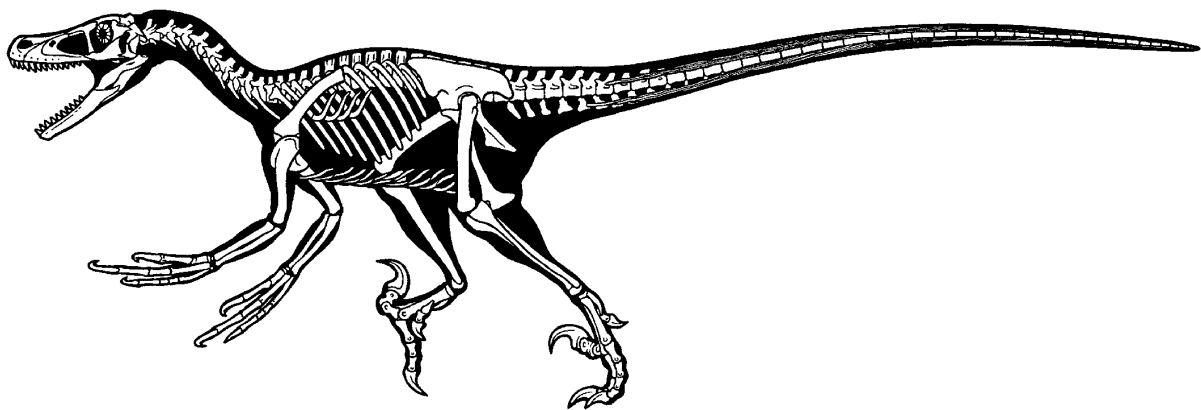
**Fig.3 Major stages in the evolution of modern avian skeletal design and function (from Sereno, 1999)**

Many skeletal innovations of critical functional importance for flight arose for other purposes among early theropods, including ① the hollowing of all long bones of the skeleton (Theropoda), ② removal of pedal digit I from its role in weight support, ③ expansion of the coracoid and sternum for increased pectoral musculature, plumulaceous feathers for insulation, ④ presence of vaned feathers arranged as primaries, secondaries and rectrices for display and/or brooding, ⑤ shortening of the trunk and increased stiffness of the distal tail for balance and maneuverability. *Archaeopteryx* remains a pivotal taxon, documenting ⑥ the acquisition of basic flight and perching function before the close of the Jurassic (laterally-facing shoulder joint, split propulsion-lift wing with asymmetric feathers, reversed hallux). Key refinements of powered flight and perching in later birds include ⑦ the deep thorax with strut-shaped coracoid and pygostyle, ⑧ the triosseal canal for the tendon of the principal wing rotator (the supracoracoid muscle), alular feathers for control of airflow at slow speeds, rectriceal fan for maneuverability and braking during landing, fully opposable hallux for advanced perching, and ⑨ the elastic furcula and deep sternal keel for massive aerobic pectoral musculature. Ornithothoracine birds diverged early into two clades: Enantiornithes ( “opposite birds”), which prevailed as the predominant avians during the Cretaceous, and Euornithes ( “true birds”), which underwent an explosive radiation toward the close of the Cretaceous that gave rise to all living avians (Neornithes, or “new birds”).

3). Now represented by hundreds of specimens, the toothless, crow-sized *Confuciusornis* has fast become the best known Mesozoic avian (Chiappe et al., 1999).

Although relatively obscure until recently, spar-

row-sized enantiornithine birds are now known to have dominated avifaunal diversity from mid through Late Cretaceous time (Fig.6). Enantiornithines were first described from Argentina (Walker, 1972; Chiappe, 1996; Sereno, 2000) and later discovered in



**Fig.4 Silhouette skeletal reconstruction of *Velociraptor mongoliensis* based on the holotype and many more recently discovered partial skulls and skeletons**  
Skeletal length approximately two meters.

the Las Hoyas beds in Spain (*Iberomesornis*: Sanz et al., 1988; Sereno, 2000; *Concornis*: Sanz et al., 1995) and Jiufotang Formation in Liaoning (*Sinornis*: Sereno et al., 1993, 2002; *Protopteryx*: Zhang and Zhou, 2000). This toothed clade of basal avians is now known from rocks around the world, although best known from lakebeds in central Spain and north-eastern China.

**2.3 Filaments to asymmetric pennaceous feathers**

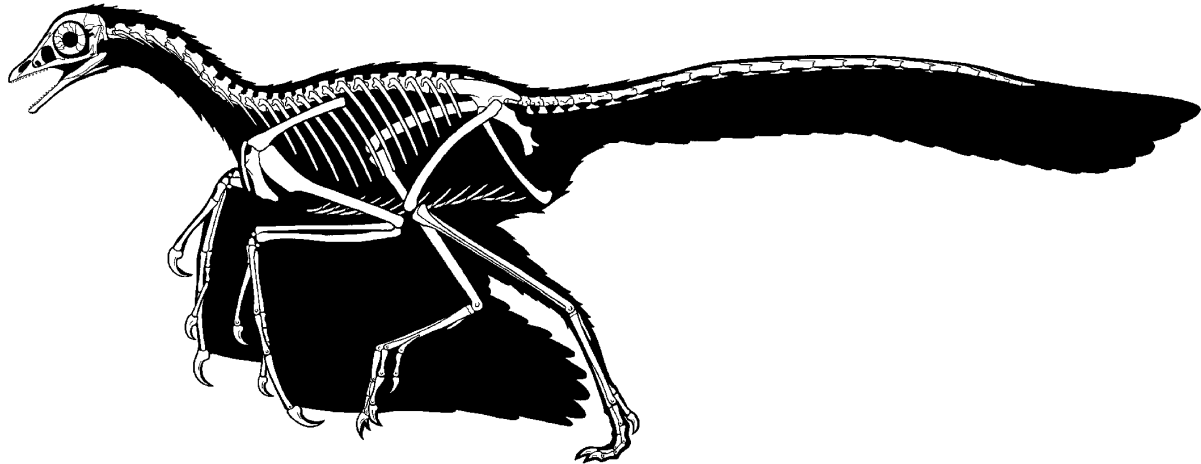
The initial discovery of integumental “fibers” in the basal coelurosaurian *Sinosauropteryx* (Chen et al., 1998) and the more advanced therizinosaurid *Beipiaosaurus* (Xu et al., 1999a) suggested simple down-like feathers but remained controversial. The discovery of longer shafted structures with herring bone pattern fore and aft removed any doubt that basal oviraptorosaurians (*Caudipteryx*: Ji et al., 1998; Zhou et al., 2000) and dromaeosaurids (*Sinornithosaurus*: Xu et al., 1999b, 2001) pos-

sessed pennaceous feathers with barbs on the limbs and tail, and that this complex feather type, thought to be unique to birds, arose first among basal maniraptorans (Fig.3).

The most remarkable finding is the presence of long asymmetric vanes on feathers composing primitive wings attached to the trailing edge of the fore and hind limbs of the small dromaeosaurid *Microraptor* (Xu et al., 2003). *Microraptor* appears to have been adapted to a semi-arboreal lifestyle that included gliding. If its status as a basal dromaeosaurid is confirmed (Hwang et al., 2002), this may have been the primitive lifestyle for the clade that included other terrestrial deinonychosaurians and volant birds (Paraves; Fig.3).

**2.4 Bigger brains**

Compared to living reptiles, birds have dramatically larger brain volumes relative to body mass, particularly in the cerebrum (forebrain). A partial endo-



**Fig.5 Silhouette skeletal reconstruction of *Archaeopteryx lithographica*, based in particular on the Berlin and Eichstätt skeletons**  
Available articulated skeletal material suggests that the wrists were unable to flex at an angle less than approximately 90 degrees.



**Fig.6 Silhouette skeletal reconstruction of sparrow-sized *Sinornis santensis*, based on the holotypic specimen**

Enlargements show early avian adaptations in the shoulder girdle and wrist (above) and sternum and tail (below).

cast of *Archaeopteryx* indicates that this increase was already in place to a considerable degree by the Late Jurassic (Jerison, 1973; Bühler, 1985). Forebrain enlargement has long been thought to characterize theropods closest to birds (Sues, 1978; Currie, 1985, 1995) but has been difficult to quantify for two reasons: the lack of complete endocasts from any of the most birdlike dinosaurs and the necessity to establish scaling relationships due to differences in body size.

Recent work focused on complete endocasts from two similar-sized Late Cretaceous theropods (*Carcharodontosaurus*, *Tyrannosaurus*) at different distances from birds. Their similar size allowed direct comparison of brain volumes free of scaling relationships (Larsson et al., 2000). *Tyrannosaurus*, an over-sized coelurosaurian, is phylogenetically much closer to birds than *Carcharodontosaurus*, an allosauroid; it has total endocast and cerebral volumes approximately 50% and 100% greater, respectively,

than in *Carcharodontosaurus*. The cerebrum in *Tyrannosaurus* is one-third, rather than one-quarter, of total endocast volume. Thus, brain and cerebral volumes do appear to have been increased significantly among theropods (coelurosaurians) more closely related to birds.

## 2.5 Invasive air spaces

The respiratory system in birds is characterized by pneumatic spaces that originate in the nasopharynx and ramify within many elements of the skull, and in air sacs from the lungs that penetrate and expand within skeletal elements. The presence of similar pneumatic structures in fossils must necessarily be inferred from bony correlates, such as smooth depressions devoid of attachment scars and openings into internal spaces.

Extensive pneumaticity of antorbital and braincase regions has occurred more than once among archosaurs but is particularly well developed in neotheropod dinosaurs and birds (Witmer, 1997).

Two systems are present, antorbital and otic, often with comparable subdivisions. Moreover, a well-developed air sac system along the axial column has arisen at least twice within dinosaurs—among basal sauropods (Wedel, 2003) and in neotheropods and their avian descendants (Britt, 1993). Air sacs in non-avian theropods open into spaces within vertebral centra via pleurocoels, and these have recently been observed in the cervical column of *Archaeopteryx* (Britt et al., 1998).

## 2.6 Muscle modifications

Some of the fore and hind limb musculature in birds is associated with characteristic scars or processes on limb and girdle bones which can be traced in extinct relatives. Two functionally significant sites for muscle attachment in the avian wing, for example, are the acrocoracoid process of the coracoid which anchors the chief flexor of the forearm (the biceps brachii), and the extensor tubercle on the medial aspect of metacarpal I which provides insertion for the extensor metacarpi radialis, the chief extensor of the carpometacarpus (Raikow, 1985). The emergence of each of these as distinct attachment sites that increase in relative size and shift in position among non-avian theropods and basal avians is well documented (Ostrom, 1976a).

In the pelvic girdle and hind limbs, most of the muscles are larger and the processes and scars marking their attachments provide a broader range of comparisons. The shift among non-avian theropods from predominantly tail-anchored femoral retractors to a less mobile femur with enhanced flexion at the knee joint is now a well-documented transformation series (Gatesy, 1995; Hutchinson, 2001).

## 2.7 Bones and body temperature

Bone histology via thin sections remains the primary means of inference concerning growth and standing metabolic rate, two physiological parameters that are substantially elevated among birds as compared to non-avian reptiles. Highly vascularized fibrolamellar bone has been shown to characterize dinosaurian embryos, juveniles and adults in a wide variety of taxa, leading to an emerging consensus that dinosaurs grew at elevated rates comparable to those in mammals and birds (Horner et al., 2001; Padian et al., 2001; Erickson et al., 2001). Some basal avians, such as enantiornithines, actually show a slightly slower growth rate with denser, less vascular bone, which may indicate precocial flight capability (Chinsamy and Elzanowski, 2001).

Oxygen isotope ratios in bone phosphate are clearly indicative of metabolic rate among extant species and also suggest that dinosaurs had elevated body temperatures and metabolic rates (Barrick and Showers, 1994). This may ultimately prove to be a

better assessment of metabolic rate than bone histology. In the meantime, the only vertebrates with growth rates as rapid as those inferred for dinosaurs from bone histology are those with elevated metabolic rates (birds, mammals). Consideration of other factors (body size, diversity, area of habitation, etc.) show that dinosaurian herbivores and carnivores grew to larger body sizes at higher species richness and within smaller areas of habitation than mammals (Farlow et al., 1995). How this was achieved remains largely unresolved.

## 2.8 Large paired eggs and brooding

The recent identification of ossified embryos within eggs has put to an end speculation about the identity of several egg types among non-avian dinosaurs. Eggs long held to belong to *Protoceratops* actually house embryos of the basal maniraptoran *Oviraptor* (Norell et al., 1994), and eggs have now been identified from embryos or from nests with associated adults for select ornithischians, sauropodomorphs and theropods (Horner 1999; Varricchio et al., 1997; Chiappe et al., 2001). Two important features of the eggs in basal coelurosaurs are their large size relative to body size in adults and their unique shell structure nearly identical to that in birds (Varricchio et al., 1997).

The discovery of intact dinosaur nests from several kinds of dinosaurs has led to two other remarkable finds regarding theropods. First, the eggs were laid serially in pairs in nests belonging to maniraptoran theropods (currently best known in *Oviraptor* and *Troodon*), in contrast to other dinosaurs in which a random arrangement of eggs in nests suggests that the eggs were laid at the same time. Varricchio et al. (1997) have suggested that maniraptorans maintained two functioning ovaries but that, like birds, laid only one egg from each ovary at a time. Birds have further reduced this pattern of serial clutch assembly to one egg from only one functioning ovary at a time. Secondly, the discovery of several intact *Oviraptor* skeletons crouched over nests of *Oviraptor* eggs (Dong and Currie, 1996; Clark et al., 1999) suggests that at least some basal maniraptorans brooded their eggs in a manner known elsewhere only in birds.

## 2.9 Diagnosing digits

Extant birds have three manual digits, the number and form of which can be traced through intermediates to *Archaeopteryx*. Like *Archaeopteryx*, basal maniraptorans (e.g., *Sinornithosaurus*, *Caudipteryx*) have three manual digits of nearly identical form, pennaceous feathers anchored on the middle digit and ulna, and a carpus shaped to form a rotary joint. This three-fingered basal maniraptoran hand and simplified carpus can likewise be traced to earlier

four- and five-fingered relatives, the latter including the basal theropods *Eoraptor* and *Herrerasaurus* (Sereno et al., 1993; Sereno, 1993). On this basis, paleontologists have long identified the manual digits in birds as I – III following Meckel (1821). Developmental biologists, on the other hand, have long identified the same digits as II – IV based on the conserved pattern of digital embryogenesis present in most extant tetrapods (Holmgren, 1955; Hinchliffe, 1985).

Recent work has unequivocally visualized the embryonic first digit in birds as a small, avascular condensation of cartilage precursors (Feduccia and Nowicki, 2002; Kundrát et al., 2002). Now all five manual digits are accounted for in the early avian limb bud, with the adult digits developing from the central three. At the same time, developmental biologists have now shown that the digital identity of the developing phalangeal series is not a stable property of condensing digital primordia, but becomes fixed during outgrowth under the influence of molecular positioning information (Dahn and Fallon, 2000). The molecular anterior-posterior positioning information involves varying concentrations of bone morphogenetic proteins which, with manipulation, can result in homeotic transformations in the phalanges, where one phalangeal series takes the form of another.

Wagner and Gauthier (1999) had earlier proposed that homeotic transfer of digital identity might have occurred within theropods—the “frame-shift” hypothesis—to explain how the very typical looking manual digits I – III of most theropods and basal birds could arise from the central three (II – IV) embryonic primordia in their extant avian descendants. Kundrát et al. (2002) noted correctly that it remains to be seen whether developmental plasticity in digital identity can be extended to the metacarpals and digital arch, as required by the frame-shift hypothesis. Then, without supporting evidence, they infer that basal birds such as *Archaeopteryx* must have undergone digital development as in extant avians and, therefore, must have descended directly from a five-fingered ancestor. Other tetrapods (many salamanders) are known to grow typical adult digits from drastically modified condensation patterns (Shubin, 1994). The nearly identical hand and feather pattern in basal maniraptorans (along with shared-derived features from every other part of the skeleton) suggests, to the contrary, that developmental biologists are just in the initial stages of understanding the molecular cues controlling digital identity in tetrapods and how these cues may be altered.

## 3 Major insights

### 3.1 “Avian” adaptations with deeper roots

Many features long held to be characteristic or unique to birds clearly have a more ancient origin among non-avian, non-volant theropods. As a consequence, they must be viewed as adaptations that originally evolved for something other than powered flight and its immediate requirements and constraints (Prum, 2002).

Skeletal features with more ancient, non-avian roots include pneumatic spaces within the axial column, uncinat processes on the ribcage, fusion of the clavicles (a furcula), increase in size of the coracoid and sternum, a rotary wrist joint, elongation of the forelimbs and hand, bowing of the ulna, elongation and enlargement of the second manual digit, retroversion of the pubis, reduction of the caudofemoralis musculature for retraction of the femur, and shortening of the tail (Fig.3). Integumental features with more ancient non-avian roots include a body covering of plumaceous feathers rather than scales, and pennaceous feathers with barbs projecting from the posterior aspect of the forelimb, hind limb, and tail. Reproductive and behavioral features with more ancient non-avian roots include avian-like eggshell structure, increase in relative egg size, serial egg assembly, and brooding.

### 3.2 Body size bottleneck

With few exceptions, non-avian dinosaurs have body masses estimated at greater than 15 kg; and several clades show long-term trends toward increasing body mass. Coelurosaurian outgroups to birds, in contrast, show a trend toward decreasing body size (Sereno, 1997). Avian flight appears to have first evolved in small-bodied species, like *Archaeopteryx*, with a body mass of less than 1 kg (Elzanowski, 2002). Clearly, powered flight evolved during a body size bottleneck, when adult body size was well below that typical for non-avian dinosaurs or the largest living volant birds (12 – 14 kg) (Pennycuik, 1989).

Early Cretaceous enantiornithines (Fig.6) were much smaller, on average, than *Archaeopteryx* (Fig.5). The perfection of avian powered flight in terms of locomotor performance (Dial, 2003a) occurred at such small body size and must have been the motor behind enantiornithine diversification during the Early Cretaceous, the first global diversification of birds.

### 3.3 Evolution of powered flight: multiple scenarios

Hypotheses for the evolution of powered flapping flight in birds have long been polarized. The “ground-up” scenario, originally articulated by Nopcsa (1907) and elaborated more recently (Ostrom, 1976b; Gauthier and Padian, 1985; Burgers and Chiappe, 1999; Garner et al., 1999; Earls, 2000; Gishlick, 2001), suggests that avian flight originated among non-volant

terrestrial bipeds. The opposing “trees-down” scenario, first articulated by Bock (1965, 1986) and elaborated by others (Feduccia, 1999; Geist and Feduccia, 2000), envisages gliding from an elevated perch as a necessary intermediate stage. Each scenario has been tied to competing phylogenetic hypotheses of avian origins, theropod or basal archosaur, respectively. Yet, such a one-to-one relationship between functional scenario and phylogenetic hypothesis has no intellectual basis, and clearly the former must be evaluated within the framework of the latter (Sumida and Brochu, 2000; Witmer, 2002).

Recent phylogenetic and functional work demonstrates these two points. The recent paleontological discoveries summarized above provide strong and consistent support for birds as derived theropod dinosaurs, their many attributes formerly thought unique to them originating at more basal levels within theropods. Functional scenarios consistent with this hypothesis, on the other hand, have diversified. Recent functional work, for example, suggests that flapping may have evolved to enhance hind limb traction in inclined running as a fundamental avian escape behavior, as currently employed in a wide variety of ground birds (Dial, 2003b). Likewise, the recent discovery of the small basal dromaeosaurid *Microraptor*—with arboreal adaptations and fore and hind limb wings suitable for gliding—has opened the door to several possible functional scenarios within the framework of a theropod origin of birds (Hwang et al., 2002; Xu et al., 2003).

### 3.4 Avian powered flight: functional modularity

Broader functional analysis of the evolution of birds as derived theropods has led to the notion of functional modularity, i. e., that locomotor function among birds is organized into three discrete functional modules (forelimbs, hind limbs, tail) with distinctive neuromuscular control (Gatesy and Dial, 1996; Dial, 2003a). The evolution of functional independence between tail and hind limb modules occurred in the transition from basal coelurosaurian theropods to basal birds. Variation in the elaboration of each of these modules, furthermore, has given rise to the diversity of avian locomotor styles, from non-volant cursors to small-bodied aerial acrobats with reduced hind limbs (Dial, 2003a).

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