JAMES A. HANCOCK
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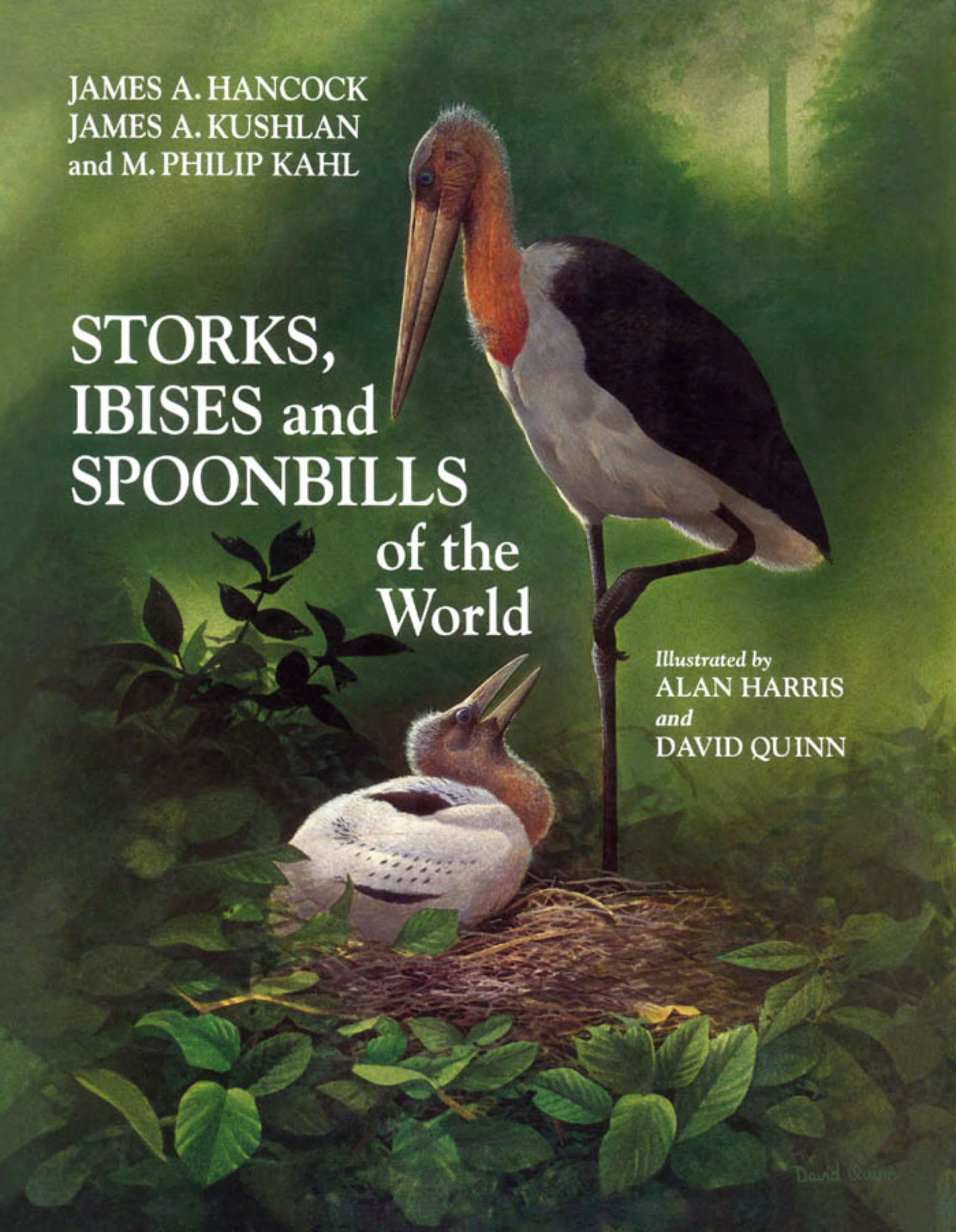
and M. PHILIP KAHL

STORKS, IBISES and SPOONBILLS of the World

Illustrated by
ALAN HARRIS
and
DAVID QUINN



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Contents

Introduction

There is no one word or concept that can describe fairly the diverse group of birds numbered among the storks, the ibises and the spoonbills. Compared to the majority of birds, they are among the larger and all have relatively long legs, necks and bills as adaptations to their fundamental way of life—walking about in shallow water. However, storks, ibises and spoonbills range in appearance from the elegant to the ungainly, in size from the moderate to the huge, and in behaviour from the flamboyant to the secretive. Their large bills may be massive or thin, straight or curved, tubular or flattened. Some species are found in large spectacular assemblies and others in crepuscular isolation. Some of the species were once widespread and common, but are now at or near to extinction. Others have always been rare, with limited ranges and highly specialized ecological niches about which little is known. Each has its own mysteries yet to be revealed, and each has its own claim on our fascination.

We have approached the task of preparing this book with some trepidation, not only because of its magnitude but also because of the growing certainty that, unlike most heron species, an unacceptable number of storks, ibises and spoonbills are facing extinction. Realization amongst the general public that much of our avian population is becoming dangerously depleted in many, if not all, parts of the world, has been slow to crystallize. Even amongst ornithologists, the true, and in many cases, horrifying situation of these species is only now becoming apparent as information pours in from remote portions of the globe. Information on rare storks, ibises and spoonbills is arriving at a rapid rate, and much of it is not encouraging.

We have attempted to include as much of this up-to-date information on the changing status of the species as possible. But again and again in preparing this book, we find ourselves emphasizing how these birds are in competition with humans for space and resources. With the world's human population expanding, the space left for large waterbirds has shrunk so rapidly in so few years that we have barely yet come to grips with the devastation that has been wrought. Two particular scenarios tend to repeat themselves among the species accounts. One is that of shy elusive species living as far away from humans as they can in areas where they have had, until recent years, little contact with people, but where they now find little habitat left. The other is of species which have lived in close proximity to humans and have very often become dependent upon them for their very survival. An example of the first scenario is Storm's Stork, about which we have learnt very little but which, because of deforestation, might well have disappeared before we had fully realized that it existed at all. The second group is epitomized by the Waldrapp Ibis which has been the recipient of every type of persecution which humans are capable of inflicting.

Today we have reached a vital stage in the relationship between humans and large wading birds. The task of conserving our environment and the birds within it can only be tackled if sufficient is known about the needs of individual species within the increasingly hostile globe upon which we live. We hope that we have managed to present as clear a picture as is possible of the precarious position of the various species of storks, ibises and spoonbills around the world and, where possible, we have suggested appropriate action to help their cause. A singular message from our review is: what is so desperately needed is protection and management of the wetland habitats that are essential to most of the species we discuss.

We have endeavoured in this book to share with the reader our own fascination and concern for these birds. We are fortunate to have been able to draw upon our own experience and that of our editors and publisher to present what we hope is a readable and authentic account of most of what is known about these species. We have been most fortunate, too, in obtaining the services of two highly talented and dedicated artists, Alan Harris and David Quinn, who have provided portraits of each of the species described. We hope this original artwork will contribute to both the enjoyment and usefulness of this monograph.

Figure 1. A Maguari Stork in full breeding plumage with two nestlings approximately 2–3 weeks old (northeastern Argentina).

Figure 2. A Glossy Ibis near its nest (southeastern Australia).

In today's financial climate, meeting the expenses of production and publication of a book of this nature, containing original plates, is thwart with difficulties. Vital to the project was the support of the Brehm Fond and Mr Wolf W. Brehm. We also are quick to acknowledge the seminal contribution to the project made by Mr Charles Luthin, working on behalf of the Brehm Fond, Vogelpark Walsrode, and the Specialist Group on Storks, Ibises, and Spoonbills. A volume such as this would have been impossible to publish at other than an astronomical price without this generous support.

We are fortunate to have been able to draw much of our information and our insight from our own experience. The authors have been privileged to travel extensively, observing these birds on each of the continents they inhabit. Between us, we have seen in the wild all but 8 of the 49 species we discuss. Two of us have spent many years studying one of the sister groups of these birds, the herons (Ardeidae), having previously summarized our knowledge in a companion volume, *The Herons Handbook* (1984). Two of us have spent many years studying the storks, spoonbills and ibises themselves, the results of which have been published in numerous papers addressed to our scientific colleagues; one having spent over 30 years studying the storks and more recently spoonbills and providing a fundamental perspective on their behaviour, ecology and taxonomy, the other, over 20 years studying populations and communities of storks, ibises and spoonbills on two continents, providing a comparative perspective on their ecology, habitat and conservation.

To supplement our own observations we have consulted an abundant although very uneven literature in an attempt to synthesize what ornithologists before us have found about the biology and conservation needs of these species. Much of this literature is excellent; and, for present and future students, we hope the extensive, yet selected, bibliography in this book will be an entrance into this literature. The bibliography is a collaborative effort, assembled by a team led by Dr Malcolm Coulter (see below). One caveat: we would urge caution and selectivity in the use of this literature, some of which goes back many years. We have attempted to be selective and to present the conflicting views, but undoubtedly will have erred in our judgement in those cases where facts we gleaned from the literature are really quite debatable.

We have also sought advice from a wide-ranging and knowledgeable host of experts. The response to our requests has been enormous, and we are deeply indebted to a very

large number of collaborators both amateur and professional who have been so supportive, encouraging and generous in sharing their insight and understandings.

Some of our trepidation is also due to our certain knowledge that no matter how thorough our own efforts, the literature, or our correspondence, a book such as this will be incomplete and in some areas will be proved incorrect. Our limitations can, and undoubtedly will, be quickly recognized. The available knowledge of the biology of these birds is highly erratic. Some species are very well known, whilst others have hardly been studied at all. Our species accounts reflect this discrepancy. Over and over again we bring to the readers' attention significant gaps in our knowledge about the most basic aspects of biology. It is the nature of such a work to summarize, synthesize, pose hypotheses, and encourage further study and testing of these hypotheses. We hope this book will inspire others to fill in the important gaps in the knowledge and to test some of the hypotheses we propose, so that the business of conservation can continue more effectively. If the book accomplishes an increased interest and study, we will be satisfied to have accomplished our primary goal.

Range maps are always troublesome. We are conscious of their summary value but have found, like many authors before us, that illustrating the ill-known and changing distribution of many species is well nigh impossible. We have, therefore, sought to show general ranges of each species, reserving for the text a more detailed description. Even here we have been handicapped by lack of precise information on the range of a surprisingly large number of species, about which little is recorded, and not least by the often unreliable recordings by collectors of the past whose poorly labelled specimens lack credibility.

Information on basic nesting behaviour is missing for some species; and, for many, information on colour changes during courtship are lacking or conflicting. Soft-part colours of museum specimens are especially unreliable guides. In the field, information on courtship colours are seldom recorded in all phases of their development. Such knowledge as we have presented should be subjected to most careful further study by field-workers who are fortunate enough to come across them. Yet for species that change the colour of their skin during courtship, this information is vital.

Voices and other noises are of importance to most of these species. Yet our understanding of their vocalizations is primitive compared to that of other birds. However, in some cases the only reliable identification of a species that can be made is by voice. These are large birds, with mostly gruff and non-melodic voices. We have rendered their calls in English inventing such words as 'Cha-cha', or 'Hunk-hunk'. These are recognizable by those who know them, but not necessarily by those who do not (in some cases, one simply had to be there).

With three authors combining their respective strengths and weaknesses, it is unfortunate that there has to be an order of authorship. Such an order does not imply the relative contribution of each. This was a true collaboration of experiences and ideas. As an Anglo-American team, we express the hope that the individual and joint efforts here presented will have brought together the sort of information which will provide encouragement and a structure for future researchers and observers.

Figure 3. A Eurasian Spoonbill head-scratching (northern India).

It is our hope, too, that the emphasis we have placed on the dire need for conservation of many of these species, and the wetland habitats on which they depend, will encourage responsible authorities to act on their behalf before it is too late.

ACKNOWLEDGEMENTS

We are extremely grateful to all those who have lent their assistance in the production of this book. As noted in the Introduction, we especially acknowledge the support of Mr Wolf W. Brehm, who has made it possible for original plates to be produced. We thank, too, our long-time colleague Mr Charles Luthin, who nurtured the project, and because of whose efforts much of the information now available on the status of these species has been gathered by field-workers throughout the world. We thank too the excellent artists, Messrs Alan Harris and David Quinn, for their outstanding contribution to the quality and usefulness of the book.

In actual production, we thank Dr Andrew Richford, our editor, Penny Robinson and Debra Kruse at Academic Press for their considerable help. We also thank especially Mrs Jane Ratliff and Mrs Bonnie Knight for their typing assistance and Mr Melvin Seid for bibliographic assistance.

We thank our colleagues who worked on the bibliography. This was a collaboration lead by Dr Malcolm Coulter to assemble a bibliography for this group of species. The present reference section is derived from the first edition of this bibliography, which is available on computer disk from Dr Coulter; the compilers of that bibliography are

Figure 4. Strawnecked Ibis. Huge flocks fly north from southern Australia after breeding.

Malcolm Coulter, Koen Brouwer, Albert L. Bryan, Jr., M. Philip Kahl, Catherine King, James A. Kushlan, Charles S. Luthin, Marcel van Wieringen, and David P. Young, Jr.

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NOTE ON RANGE MAPS

The following colour coding has been adopted. Areas where the species concerned is a breeding resident are shown in **blue**. Where a species is completely or partially migratory, the breeding range is shown in **red** and the non-breeding range in **green**. Arrows indicate principal migration routes and **?** areas where the status is doubtful.

Classification

A SYSTEM FOR CLASSIFICATION

We are able to understand the world around us in part through our ability to classify objects and events into manageable units and by establishing, in our mind at least, logical relationships among them. This is especially true of the natural world; the classification of living beings is a specialized science called Taxonomy or Systematics. As in our everyday efforts at pigeon-holing objects and ideas, the scientific system of classifying organisms also has two goals, to identify and name the entities of the natural world and also to describe the relationships among them. In developing a classification, taxonomists seek to place together organisms that are related through descent from a common ancestor. Such organisms share a common genetic inheritance that we expect to be expressed in various characteristics that we can see or measure. Of course, characteristics may in fact, be similar without being derived from genes shared with a common ancestor, and, conversely, there is no reason to suspect that all genetic similarity should be expressed in characteristics we can easily observe or measure. An increasing ability to discern biochemical differences, including characteristics of the DNA itself, provides additional measures of genetic similarity.

The basic unit of taxonomy for organisms such as birds is the species. For sexually reproducing organisms, a species consists of the various populations of individuals that are potentially capable of breeding with each other and producing offspring that are not at such a disadvantage that they in turn cannot breed successfully. The species itself is identified by two latinized names, the genus name followed by the specific epithet, as for example in the scientific name for the Sacred Ibis, *Threskiornis aethiopicus*.

Acceptability of names is governed by codified rules, especially the rules of priority—the first valid name proposed for an organism is the name everyone is expected to use. Determining the right name to use is sometimes but not always straightforward. Sometimes what constitutes the original description is debatable; species repeatedly have been reassigned among genera as new information and opinions about their relationships emerge. So most species have gone by various names since their discovery. In each species account, the scientific name and information on the source of the original description are given, as is the identity of the taxonomist credited with naming the bird. This attribution is placed in parentheses if the genus to which the species is assigned has changed since description.

Unlike scientific names, common names vary from place to place and from language to language. There has been some effort to standardize common names in various geographic regions, where technical committees deliberate and provide lists of recommended usages. In each species account, we make an effort to provide the reader with some of these names. There is, however, no 'right' or 'wrong' common name, and some species have a score of names in several languages. The English names we use, we recommend for their clarity within context of the stork–ibis–spoonbill group worldwide.

Over wide geographic areas populations of some species may diverge into recognizably different kinds of organisms but yet be fully capable of interbreeding. These distinguishable geographic entities are often called races or subspecies. Subspecies may be named, should it be useful to do so. For example the Sacred Ibis of Africa is *Threskiornis aethiopicus aethiopicus*, whereas the isolated birds of Madagascar are *Threskiornis aethiopicus bernieri*. In most cases, populations are not named, even though we can expect variation to occur among populations scattered over wide areas of the globe.

What population should be considered a species and what a subspecies is often unclear, and so may be contentious. Interbreeding potential is what marks a species. Members of two different species would not interbreed if they occurred together; members of the same species or two subspecies of the same

species would; however, since they do not occur together, proof of their compatibility is usually lacking. To be considered a subspecies, a population must be distinctive yet potentially interfertile with other subspecies and capable of producing offspring that are not at a disadvantage in nature. (A species having more than one subspecies is called polytypic.) One should keep in mind that the more fundamental question of interest is not whether a population has a subspecies name, but rather what are the biological implications of the variation of characteristics among populations.

Species that are similar, and obviously closely related, that are found in disjunct ranges are called allospecies and considered members of a superspecies. The Sacred Ibis, Oriental White Ibis, and Australian White Ibis are members of a superspecies, in our classification scheme.

The reproductive isolation of individuals of two species results from differences in morphology, behaviour, biochemistry and, ultimately, genetics. These all provide criteria by which we too can identify various species, and also the criteria upon which are based the higher classifications, which attempt to express the genetic similarities that derive from sharing common ancestors.

The genus name is a low-level way to provide an indication of relationships among species. Species that share the same genus name are more closely related to each other than they are to species in other genera. That is, species sharing a genus name also share a common ancestor, and a genetic similarity, not shared with other species.

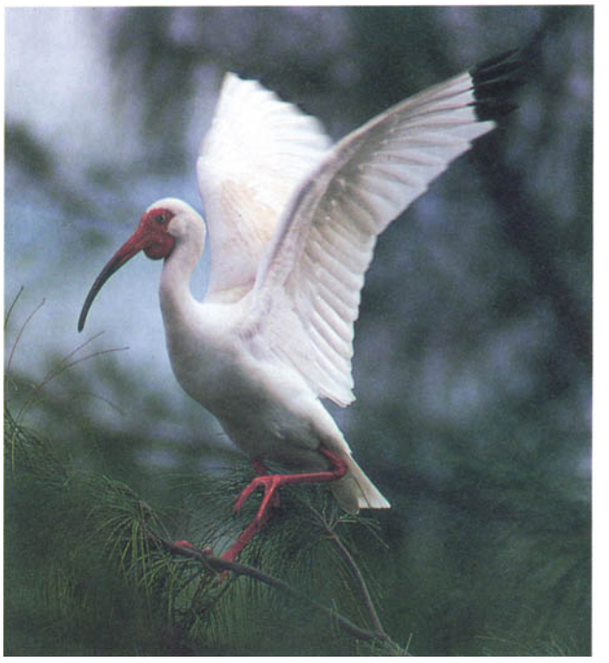


Figure 5. An American White Ibis in breeding plumage, with gular-sac inflated (southeastern USA).

Figure 6. American White Ibis. Immature (left) and adult (southeastern USA).

Higher-level classification proceeds in the same manner, with related genera being grouped into families, families into orders, orders into classes, classes into phyla, and phyla into kingdoms. To show finer relationships, primary taxa can be further subdivided into higher and lower groups, such as suborder (below order), subfamily and tribe (below family) or superspecies (above the species). In some detailed classification schemes, there may be many more taxa used to show details of relationships. Above the species level, classifications become increasingly a matter of professional opinion; although modern techniques of biochemical genetics and cluster analysis can make the process of seeking similarities more objective, questions of convergence nevertheless remain.

STORKS, IBISES AND SPOONBILLS

Who, then, are the storks, ibises and spoonbills? According to currently accepted working classifications, storks, ibises and spoonbills share a common classification down to the ordinal level. They are animals (kingdom Animalia), chordates (phylum Chordata), birds (class Aves), and wading birds (order Ciconiiformes). Which birds and which groups are additionally included in the order Ciconiiformes is, however, a matter of considerable debate in the pages of the scientific literature.

The storks, ibises, spoonbills, herons and others are identifiable in part by their long legs and long necks, both adaptations for foraging by wading about in shallow water. These few characteristics of obvious ecological importance may seem to be rather slim branches on which to hang a taxonomic relationship. However, this intuitive grouping has held up to repeated scrutiny since Linnaeus in 1758, and we can be reasonably confident that the characteristics represent a fairly robust adaptive strategy.

Other characteristics of the storks, ibises and spoonbills relate to the adaptive strategy of being a 'wading bird'. Their long necks have 15–20 vertebrae, and are capable of considerable mobility, as would be expected to be able to feed. Their tibiae and tarsi are unfeathered, and toes are elongated, often slightly but never fully webbed, with the lengthened back toe (hallux) also expected of a wading bird. Some groups sport toenails specialized for feather maintenance. They also have other characters in common (T.H. Huxley 1867, Baird et al. 1884, Coues 1903, Witherby et al. 1939), such as similar sterna, palates and syringes, minute intestinal caeca, elongated bills, long, broad and rounded wings, and short tails. But other birds also have some of these characteristics. They also share such common morphological features as particular conformations of carotid arteries and bony palate, which however are not unique to these birds. The sexes are identical in plumage; but females are, to a greater or lesser degree, smaller than males. Many species nest in colonies and all have helpless (altricial) young that adults feed in the nest.

In addition to the similarities, the groups of birds traditionally included in the order differ in aspects of behaviour and morphology. It is, in fact, not possible to enumerate obvious morphological characteristics that definitively separate these species from other birds, some of which may or may not be included in the order. This deficiency has led to considerable debate, over the past 50 years, as to which birds should be included in the Ciconiiformes (see Sibley and Ahlquist 1972 and 1990 for further discussion). Storrs Olson (1979) concluded that it was an artificial assemblage. Alan Feduccia (1980) has suggested that resolution of the phylogenies of the groups currently included in the Ciconiiformes remains one of the major challenges of contemporary evolutionary ornithology. Either way, the use of biochemical characteristics has gone a long way to increasing our confidence in the close relationships among birds in the traditional ciconiiform groups.

The concept of a ciconiiform taxon has a long and distinguished history. T.H. Huxley (1867) suggested a group, which he called Pelargomorphae, that included the ibises and spoonbills, storks, herons and flamingos. This was the basic view of Gadow and of Wetmore, who produced the classification scheme that for almost a century has been the basis for the modern consensus of avian classification. Wetmore's (1960) Ciconiiformes was subdivided into four suborders for the herons, the Shoebill, the storks, ibises and spoonbills, and the flamingos; these are the 'traditional ciconiiforms'. The herons were further divided into two

Figure 7. A Royal Spoonbill with crown feathers fully erect (southeastern Australia).

families, the typical herons (Ardeidae) and the Boatbilled Heron (Cochleariidae). The storks (Ciconiidae) and the ibises/spoonbills (Threskiornithidae) were in their own individual families, as was the distinctive Hamerkop (Scopidae). Wetmore's classification, minus the flamingos, was similar to that proposed about the same time by Verheyen (1959) and was congruent with one of the first applications of biochemical genetic data by Sibley (1960a,b).

Since then, other studies have been conducted, including a proposed revision of the classification of the world's birds, based on biochemical and other evidence, by Charles Sibley and his associates (Sibley et al. 1988, Sibley and Ahlquist 1990, Sibley and Monroe 1990). These studies, in one sense, produced a radically different view of the Ciconiiformes, a more encompassing view that includes within the order other groups. Many of these have previously been suggested to be related in one way or another, but they were generally retained in other orders. At the same time, taxa have been removed from previously recognized orders, implying that these were not natural assemblages. This expanded ciconiiform order included, in addition to our groups, such groups as the waders (i.e. shorebirds), gulls and terns, hawks, grebes, tropicbirds, boobies, anhingas, cormorants, herons, the Hamerkop, flamingos, pelicans, New World vultures, frigatebirds, penguins, loons, petrels, and albatrosses.

In another sense, these studies have been comforting in that nestled within the expanded Ciconiiformes are the herons, storks, ibises and spoonbills, which continue to be perceived as being related at some level between family and order.

It is useful to draw a distinction between a classification and a species sequence (Bock 1990). A classification is a three-dimensional tree of relationships that ideally reflects the phylogeny (i.e. the evolutionary relationships) of the group (Sibley and Ahlquist 1990). A sequence is an ordered list of taxa, derived from a classification schema. A standard sequence is a heuristic device that facilitates communication, and is not tampered with lightly (Mayr 1989, Bock 1990). In this monograph we have followed the standard species sequence of Peters' (1931) Check-list (Kahl 1979a,b, J. Steinbacher 1979), to the fullest extent possible given the new understandings of species limits adopted in this book.

Questions about Ciconiiform Taxonomy

All classification systems are really the expression of a series of hypotheses that provide the basis for new questions and new hypotheses (Sibley et al. 1988). Some of the principal taxonomic questions exposed by proposed classifications include: the relationships of the flamingos; the relationship

Figure 8. A female Yellowbilled Spoonbill performing the Greeting Display (southeastern Australia).

Figure 9. A Marabou Stork yawning at its nest (northwestern Kenya).

of the herons to the other groups; the most appropriate classification of the Hamerkop; the most appropriate classification of the Shoebill; the boundaries of the order with respect to possibly related taxa such as pelicans and their relatives, New World vultures, and hawks; and the family and generic relationships among the various species within the constituent groups of the traditional ciconiiforms.

The relationship of the flamingos has been an especially controversial question, particularly because they show morphological similarities to ciconiiforms, waterfowl and waders. The question of interest in our context is whether the similarities they show to other long-legged wading birds might be due to convergence or to shared ancestry. Sibley and Ahlquist (1972) concluded that flamingos were indeed ciconiiforms and that flamingos linked the wading birds and the waterfowl. Feduccia and Olson (Feduccia 1978, 1980, Olson 1979, Olson and Feduccia 1980), on the other hand, argue from palaeontological and other evidence that shorebirds constitute the ancestral group of both the flamingos and the waterfowl, and that none of these groups is particularly closely related to the ciconiiforms. On the basis of their studies of DNA, Sibley and Ahlquist (1990), however, conclude that flamingos are indeed relatively closely related to other members of the heron–stork–ibis cluster of birds.

The herons are, by all accounts, closely related to each other (Payne and Risley 1976). They have distinctive, narrow feather tracts and patches of powder-down feathers, a completely feathered head, seasonal development of elongated display plumes, a narrow skull, a long, straight bill, a modified 6th cervical vertebra that allows the neck to be held in an S-shape in flight, a comb-like (pectinate) middle toenail, and young with a single down coat. Hancock and Kushlan (1984), in a companion volume to the present monograph, provided a synthesis of the biology and classification of the group, the latter mostly derived from the studies of Payne and Risley (1976) and Payne (1979), although retaining several traditionally generic allocations pending further study.

One of the longstanding issues regarding the heron group relates to the distinctive Boatbilled Heron *(Cochlearius cochlearius)*. Hancock and Kushlan (1984) suggested that it should be grouped with the night herons. Sheldon (1987) more recently provided biochemical evidence for a subfamilial relationship between the Boatbilled Heron and tiger-herons, and no distinction between day and night herons. Despite these finding, the linear arrangement of taxa by Payne and Risley (1976) and the overall integrity of the heron family continues to remain intact. If anything, recent studies have tended to find the Boatbilled Heron to be less distinctive from the other herons than previously thought.

However, the relationships of herons to other wading birds has not been so well settled. Olson (1979) suggested that they show few morphological similarities to the other traditional ciconiiforms and are the only currently successful representatives of an early radiation of crane-like birds not clearly related to modern storks or ibises. He considers the family to be one of uncertain affinity (Olson 1985a,b). Biochemical genetic evidence continues to support their ciconiiform heritage and a relationship at some level within

Figure 10. Abdim's Storks at their nest on a rocky island in Lake Shala (southern Ethiopia).

the order to ibises and storks (Sheldon 1987). More specifically, this evidence suggests that herons, the Hamerkop, flamingos, ibises, storks, the Shoebill and pelicans are descended from a common ancestor (Sibley and Ahlquist 1990).

The Hamerkop (*Scopus umbretta*) is a small bird, lacking the long legs and neck characteristic of the other traditional ciconiiforms. We have found that it flies, perches, feeds, nests, and engages in courtship, all in distinctive ways (Kahl 1967b, 1979c). As noted above, biochemical evidence (Sibley et al. 1988) suggests that it is related to the herons, storks and ibises, but it certainly is not a true stork. Because of its distinctiveness, we have chosen not to treat the Hamerkop in the present monograph.

The Shoebill (*Balaeniceps rex*) shares anatomical characteristics with the true storks, including a distinctive tubular ear bone (Feduccia 1977) and a Bill-clattering Display (Kahl 1972e). It also differs in other respects. For example, we found that it did not excrete on its legs for cooling (Kahl 1967a) and its chromosomes differ from those of the true storks (De Boer and Van Brink 1982). It shows many similarities to pelicans (Cottam 1957, Feduccia 1977, Saiff 1978, Olson 1979, 1985b). Sibley and Ahlquist (1972) considered the species to be a ciconiiform, and Feduccia (1977) considered it to be a stork. Kahl (1979a) and Olson (1985b) assigned it to its own family adjacent to the true storks. Sibley and Ahlquist (1990) proposed that, within their much expanded Ciconiiformes, it is most closely related to pelicans, and with the pelicans is placed in a superfamily between the superfamily that includes the ibises and the one that includes the storks and New World vultures. Because of

Figure 11. A Lesser Adjutant Stork feeding its young (northeastern India).

its historical identification with storks, we have chosen to include it in this monograph.

Although the boundaries of the order Ciconiiformes continue to be debated, there emerges a clear consensus regarding the storks, ibises and spoonbills. From the morphology-based classifications of Huxley and Wetmore, through the various behavioural studies such as some of our own, to the biochemical studies of Sibley and others, these three groups of birds are repeatedly found to be related. Analysis of DNA hybridization similarities indicate that herons, the Hamerkop, flamingos, ibises and spoonbills, storks, New World vultures, pelicans, and the Shoebill are more closely related among themselves than they are to other groups of birds and so are descended from a common ancestor.

Sibley and Ahlquist (1990) describe well the probable history of this group. Each is a result of a radiation exploiting an unoccupied niche, each showing its own way of life. Each flourished, and spread widely, retaining characteristics of their common ancestry in their morphological and genetic similarities.

In this monograph, continuing our evaluation of the biology of these groups that began with *The Herons Handbook* (Hancock and Kushlan 1984), we summarize the biology of the storks, the ibises, the spoonbills and the Shoebill.

Relationships within the Storks

The typical storks are a distinctive group sharing a number of characteristics, including long legs with half of the tibia bare, relatively short toes with small webs, 12 tail feathers, 12 primary feathers (the 12th being minute and/or lacking in the wood storks and openbills), bare portions on the head, feathered oil gland, a common musculature of the pectoral associated with soaring flight (Vanden Berge 1970), a stout bill, predominantly simple black and white plumage colours, young with two down coats, large air sacs under the neck skin, and a lack of powder down. They also have behaviours in common, including cooling their legs by defecating on them (Kahl 1963b), a trait they share with the New World vultures (Ligon 1967). Olson (1985b) and Sibley et al. (1988), and others before them, suggested that they are closely related to the New World vultures, and Sibley and Ahlquist (1990) included the vultures in the same family as the storks, remarking that they had been taxonomically misplaced for two centuries.

The most recent classifications of stork species are based on behaviour (Kahl 1979b), anatomy (D.S. Wood 1983), and a combination of the two (D.S. Wood 1984). These studies have grouped the species in fewer genera than was previously the case (Kahl 1972e). We draw from the results of both sets of studies in recognizing two higher level divisions of the true storks, the wood storks and the openbills in the tribe Mycteriini, and the typical storks, giant storks and adjutants in the tribe Ciconiini. We have chosen to use tribes in subclassifying the storks, rather than the more traditional rank of subfamily, because the proper taxonomic rank of the typical stork group remains under discussion as does the appropriate positioning of the Shoebill and New World vultures. Sibley et al. (1988) classify the traditional storks as a subfamily, in which case tribe would be the next lower taxon. In the present monograph, we continue the more traditional approach of considering the storks to represent the family Ciconiidae.

The stork tribe Mycteriini includes four wood storks (*Mycteria*) and two openbill storks (*Anastomus*). All locate food primarily by touch rather than by vision, and have bills especially, and even uniquely, suited for this behaviour.

The wood storks have large, cylindrical, but slightly down-curved bills, which they place in the water and hold open for fish to swim into. They also use special movements, such as pumping their feet or opening and closing their wing, to increase the likelihood of a fish entering the bill. *Mycteria* have distinctive displays including aerial Flying

Around, a Gaping Display, and Display Preening (see subsequent chapters for descriptions of these and other behaviours). Courtship includes a gaping and snapping of the bill but not the Bill-clattering characteristic of other storks. The differences among the *Mycteria* storks are minor, consisting primarily of plumage and soft part coloration (Kahl 1972b). It is interesting to note that one of the wood storks, the Yellowbilled Stork, is called *Mycteria ibis*. Through the vagaries of nomenclatural history, the rules of priority result in the name 'ibis' being given not to an ibis, but to a stork (Mathews 1913).

The openbills have bicurved bills that leave a central gap. Where they come together at the tip, the curved mandibles form a forceps with which the stork pincers its preferred and almost exclusive prey, freshwater snails. The two species are markedly different in colour, *Anastomus lamelligerus* being black and *Anastomus oscitans* being mainly white. The two possess an Advertising Sway behaviour that seems to be unique (Kahl 1972d); during copulation the male shakes his head rather than clattering his bill.

In the tribe Ciconiini, we include 13 species in the genera *Ciconia* (typical storks), *Ephippiorhynchus* and *Jabiru* (giant storks), and *Leptoptilos* (adjutants). D.S. Wood (1984), arguing on the basis of his quantitative analysis of character distance, deviated from Kahl's (1972e) classification by including the genera *Ephippiorhynchus* and *Jabiru* in a tribe with the typical storks. This reflects the undoubted affinities between the genera *Ciconia* and *Ephippiorhynchus*. However, the *Jabiru* also shares characteristics with the adjutants, and is somewhat of an intermediate between the other two giant storks and the adjutants. In that the classification scheme should reflect that intermediacy, it seems to us that a more natural classification is achieved by grouping all four genera into one tribe, Ciconiini.

The typical storks, members of the genus *Ciconia*, have straight or slightly recurved bills; the head and neck are feathered, but the skin around the eye (lores) is bare. A display, the Head-shaking Crouch, performed by the male is found uniquely in the genus *Ciconia* (Kahl 1971f, 1972c). Bill-clattering and whistling vocalizations are characteristic, especially in courtship. We have concluded that the Black Stork is the most primitive and the White Stork the most advanced in the genus *Ciconia* (Kahl 1972c). Abdim's seems closely related to the Black Stork, both behaviourally and morphologically. The Woollynecked Stork of Africa and Asia and the Maguari of South America share a number of characteristics, including a forked black tail. We here recognize the Storm's Stork (*Ciconia stormi*) as a separate species from the Woollynecked Stork and the Oriental White Stork (*Ciconia boyciana*) as a separate species from the White Stork.

Figure 12. Asian Openbill Storks sunning (northern India).

Fossils of this group are known, including both extant and extinct species of *Ciconia* as early as the middle Miocene and as late as the late Pleistocene in Africa (C.J.O. Harrison 1980).

In the giant stork genera *Ephippiorhynchus* and *Jabiru*, a Flap-dash Display is used by pairs on the feeding grounds. The Blacknecked and Saddlebill Storks are similar in many ways to the typical storks. The Jabiru shares an inflatable throat sac with the adjutant storks. Additionally, the Saddlebill Stork has a vascularized chest patch. Because of its intermediacy between the typical storks and the adjutants, unlike D.S. Wood (1984), we have retained it in its own genus. The adjutants (*Leptoptilos*) all feed to some degree as scavengers, have massive bills, and lack normal contour-feathering on the head and neck, both adaptations for eating large carrion. They are unique in giving a loud squealing or mooing vocalizations during courtship (Kahl 1966a, 1970, 1972a). The large inflatable throat sac is an obvious characteristic of these storks.

Relationships within the Ibises and Spoonbills

Ibises and spoonbills are medium-sized birds that have been recognized as being related since at least the mid 1800s (Nitzsch 1840). They are almost always grouped at the family level (Sibley and Ahlquist 1972, 1990). The most widely used name for the group is the Threskiornithidae (Eisenmann et al. 1984). It has been argued that by priority the more appropriate name is Plataleidae (K.E. Campbell 1986, A.R. Phillips 1986, Olson et al. 1986). However, following W.J. Bock (pers. comm. 1990) in his advocacy of retaining the well-used name, as well as by priority, we continue to use 'Threskiornithidae'.

Figure 13. A Woollynecked Stork shading its young at the nest (northern India).

The notable differences in bill morphology have long resulted in the recognition of two subfamilies, the Threskiornithinae including the ibises, having a narrow downcurved bill with a flattened tip, and the Plataleinae including the spoonbills with a flattened bill. The two bill types correlate with the predominant non-visual feeding modes adopted by the two groups, Probing and Head Sweeping, respectively (Kushlan 1978a). The various species have a number of characteristics in common, especially a distinctive slit-like cranial morphology (called schizorhinal), which they share with waders (perhaps by convergence) and which is an adaptation to allow upper bill movement. They also have a distinctive musculature and sternum, 11 primary feathers (11th minute), 12 tail feathers, long legs with lower half of tibia bare, loss of feathers on the head and even neck, distinctive ornamental plumes, and changeable soft-part colours. They lack powder-down patches, have a cupped middle toenail undoubtedly used for feather maintenance, and a grooved mandible that functions in removing secretions of the supraorbital salt gland. They have down on both feather tracks and non-feathered portions of the skin (apteria). An interesting aspect of the biology of ibises is the variability of chromosome structure among some species, a very unusual trait among birds (including storks) in which chromosomal uniformity is the rule (Capanna et al. 1982).

In addition to the traits they share with storks, the ibises and spoonbills share characteristics with the waders, traditionally classified in the order Charadriiformes. Olson (1985b) included ibises and waders in the same order. However, a relatively close relationship is not supported by DNA evidence (Sibley and Ahlquist 1990).

The ibises and spoonbills have been relatively little studied in the field because they are hard to observe and the various species are well scattered around the world. Extremely little is known about certain rare or inaccessible species.

The ibis subfamily Threskiornithinae consists of 23 species distributed among 14 genera. It is likely that the present classification does not adequately represent relationships among the species. However, taxonomically useful anatomical trends among the species are not readily apparent. It is also an old group, dating back to the Miocene, about 25 million years ago. The earliest fossils are assignable to a still living genus, the widespread *Plegadis* (*Plegadis peganus* and *Plegadis pharangitus*—Olson 1981). Species representing two other living genera are known from the Pliocene of South Africa, *Geronticus apelex* and *Threskiornis aethiopicus*, the bones of the latter being indistinguishable from the modern form that occurs in the area today (Olson 1985a). Extinct species of present genera (*Theristicus wetmorei* and *Eudocimus peruvianus*) are known from the Pleistocene in South America (K.E. Campbell 1979). Especially intriguing are subfossils of flightless ibises, *Apteribis glenos*, from the islands of Maui and Molokai in the Hawaiian Islands and Jamaica (*Xenicibis xympithecus*) (Olson and Wetmore 1976, Olson and Steadman 1977, 1979, Olson and James 1991),

which indicate the occurrence of very recent extinctions of particularly vulnerable species of ibis. The Hawaiian forms were undoubtedly lost through the hand of man.

Relationships among the ibis genera are not well understood. The glossy ibises (*Plegadis*), represented so anciently in the fossil record, today have a nearly worldwide distribution, the only ibis genus to do so. The Glossy Ibis itself (*Plegadis falcinellus*) is found on all inhabitable continents and may be a relatively recent invader of the New World. The Whitefaced Ibis is the South American and western North American form, whereas the Puna Ibis is a South American montane form.

From available fossil and osteological evidence, it appears that the genus *Eudocimus* is closely related to the glossy ibises (Mayr and Short 1970, Olson 1981). The genus has traditionally been considered to include two forms, the American White Ibis (*albus*) ranging from North America to northern South America and the Scarlet Ibis (*ruber*) found in northern South America. Because their recent studies demonstrated considerable successful interbreeding of red and white birds in a natural zone of overlap, Ramo and Busto (1987) concluded that, by definition, the two forms must be considered the same species. This conclusion is supported by other evidence, not the least being that the presence of the carotenoid pigment canthaxanthin, which accounts for the colour of the red form, is unreliable as a taxonomic characteristic (Sibley and Ahlquist 1990).

South America is a centre of ibis radiation. Most species there are at this time assigned to unique genera, reflecting the dearth of information available on extant and fossil South American forms, lack of taxonomic study of the subfamily as a whole, and the probable age of the group. *Theristicus* is here considered to include a single polytypic species. The genera *Phimosus, Cercibis, Harpiprion, and Mesembrinibis* are also represented by single species. Sibley and Ahlquist (1990:852) present the intriguing result of one experiment: that there may be a split within the family between the South American genera (*Mesembrinibis, Theristicus, Cercibis, Eudocimus*) and the Old World ibis genera and spoonbills. This deserves further study.

The sacred ibises (*Threskiornis*) are widespread in the Old World. Once divided into four species, they were combined into two species and many subspecies by Holyoak (1970). More recent studies of their behaviour, structure, and chromosomes suggest that three species exist (Cramp 1977, De Boer and Van Brink 1982, Mees 1982, Lowe and Richards 1990). In this monograph we restore the division of this genus into four species, three of which are allospecies. De Boer and Van Brink (1982) suggested that the Australian White Ibis (*Threskiornis molucca*) may be the ancestral form from which the other two species were derived.

Several species of ibis of Africa, Madagascar and the

Figure 14. A Strawnecked Ibis in breeding plumage (southeastern Australia).

Figure 15. Black Storks at their nest; male nearest the camera (southwestern Poland).

Figure 16. A Shoebill in a grassy marsh adjoining Lake Kyoga (north-central Uganda).

Middle East are included in the genera *Bostrychia, Lophotibis*, and *Geronticus*. It is likely that these are fairly closely related to each other (Fry et al. 1985). Three genera of ibises are found only in Asia, *Pseudibis, Thaumatibis*, and *Nipponia*. Olson (1985b) suggested that *Pseudibis* is anatomically very similar to and possibly congeneric with *Geronticus*. Although the Giant Ibis has most recently been considered to be a *Pseudibis* (Holyoak 1970), Olson (1985b) has cautioned against removing this distinctive, large ibis from its specialized genus without anatomical study. We have followed this sensible advice and restore it to its separate genus.

The spoonbill subfamily Plataleinae has a cosmopolitan, although somewhat patchy, distribution. Four of the Old World species are closely related, and largely replace each other geographically. We here identify the Royal Spoonbill (*Platalea regia*) as a separate species, based on our recent studies of its behaviour and morphology, which differ from the Eurasian species (Kahl 1988a). The specific distinctiveness between the Royal and Blackfaced spoonbills (*Platalea minor*) also needs scrutiny. The New World Roseate Spoonbill (*Platalea ajaja*) and the Australian Yellowbilled Spoonbill (*Platalea flavipes*) are more distantly related to the other spoonbills, and may be most closely related to each other (Kahl 1988a).

Species Sequence of the Storks, Ibises and Spoonbills

Family Ciconiidae—the true storks

Tribe Mycteriini—the wood storks and openbills
- *Mycteria americana*—American Wood Stork
- *Mycteria cinerea*—Milky Stork
- *Mycteria ibis*—Yellowbilled Stork
- *Mycteria leucocephala*—Painted Stork
- *Anastomus oscitans*—Asian Openbill Stork
- *Anastomus lamelligerus*—African Openbill Stork

Tribe Ciconiini—the typical storks, giant storks and adjutants
- *Ciconia nigra*—Black Stork
- *Ciconia abdimii*—Abdim's Stork
- *Ciconia episcopus*—Woollynecked Stork
- *Ciconia stormi*—Storm's Stork
- *Ciconia maguari*—Maguari Stork
- *Ciconia ciconia*—White Stork
- *Ciconia boyciana*—Oriental White Stork
- *Ephippiorhynchus asiaticus*—Blacknecked Stork
- *Ephippiorhynchus senegalensis*—Saddlebill Stork
- *Jabiru mycteria*—Jabiru Stork
- *Leptoptilos javanicus*—Lesser Adjutant Stork
- *Leptoptilos dubius*—Greater Adjutant Stork
- *Leptoptilos crumeniferus*—Marabou Stork

Family Balaenicipitidae—the Shoebill
- *Balaeniceps rex*—Shoebill

Family Threskiornithidae—the ibises and spoonbills

Subfamily Threskiornithinae—the ibises
- *Eudocimus ruber*—American White Ibis
- *Phimosus infuscatus*—Barefaced Ibis
- *Plegadis falcinellus*—Glossy Ibis
- *Plegadis chihi*—Whitefaced Ibis
- ***Plegadis ridgwayi*—Puna Ibis**
- *Cercibis oxycerca*—Sharptailed Ibis
- *Harpiprion caerulescens*—Plumbeous Ibis
- *Theristicus caudatus*—Buffnecked Ibis
- *Mesembrinibis cayennensis*—Green Ibis
- *Bostrychia hagedash*—Hadada Ibis
- *Bostrychia carunculata*—Wattled Ibis
- *Bostrychia olivacea*—Olive Ibis
- *Bostrychia rara*—Spotbreasted Ibis
- *Lophotibis cristata*—Madagascar Crested Ibis
- *Threskiornis aethiopicus*—Sacred Ibis
- *Threskiornis melanocephalus*—Oriental White Ibis
- *Threskiornis molucca*—Australian White Ibis
- *Threskiornis spinicollis*—Strawnecked Ibis
- *Geronticus eremita*—Waldrapp Ibis
- *Geronticus calvus*—Bald Ibis
- *Pseudibis papillosa*—Black Ibis
- *Thaumatibis gigantea*—Giant Ibis
- *Nipponia nippon*—Oriental Crested Ibis

Subfamily Plataleinae—the spoonbills
- *Platalea leucorodia*—Eurasian Spoonbill
- *Platalea regia*—Royal Spoonbill
- *Platalea minor*—Blackfaced Spoonbill
- *Platalea alba*—African Spoonbill
- *Platalea flavipes*—Yellowbilled Spoonbill
- *Platalea ajaja*—Roseate Spoonbill

Conservation

How unfortunate it is that large water birds are particularly subject, either intentionally or otherwise, to continual attack from the human race. They are hunted, they are eaten, they are harassed, their feeding habitat is altered, their nesting sites are destroyed. On the other hand, they are also appreciated, for their size, their beauty or ugliness, or for the place many hold in the culture and history of a people.

In our studies of the herons of the world, we were constantly amazed at the resilience of members of that family (Hancock and Kushlan 1984). In our work on the present volume, we found that for storks, ibises and spoonbills the story is a very different one. These birds have come under much the same pressures as have herons, but for reasons not quite clear, except as explicated for an individual species, they have responded poorly to the changes imposed upon them. A result is that many species of this diverse group of birds are at, or near extinction, over much of their former range (W.B. King 1981, Collar and Andrew 1988).

In many areas, these bird populations are suffering from a combination of pressures including deliberate killing, deforestation, wetland drainage, use of intensive modern farming methods, and the accumulative effects of pesticides (J.F. Parnell et al. 1988). These problems seem universal, though the degree to which they apply varies according to the awareness and concern of the human inhabitants of the region. In fact, almost invariably for these large birds, it is the attitude of the local human population that decides whether a species survives in its midst.

Solutions are by no means unclear, although they may be difficult to put into practice; J.F. Parnell et al. (1988) discuss these. Habitat improvement is required to reverse the impact of wetland destruction and alteration. In many cases improvement will require direct manipulative management of water, vegetation and breeding sites in compensation for loss of natural feeding and nesting sites, as well as monitoring and protection of existing functioning ecosystems (Kushlan 1979b, 1983, 1987, 1989a,b). More general environmental improvements are also required, especially regarding the long-term effects of chemical contaminants. It has been noted that 'People control is a foremost aspect of colonial waterbird management' (J.F. Parnell et al. 1988), and control of disturbance, including both passive disturbance and hunting, is needed, especially at colony sites. In some cases it is necessary to consider management to reduce natural interactions, such as predation and competition, for crucially endangered species. Multispecies fishery management is required in those areas where the needs of these birds are at odds with those of human fisheries. In some cases, the enhancement or re-establishment of a population may require reintroduction of birds, from wild or zoo stocks, and the artificial establishment of suitable nest or colony sites (e.g. Hirsch 1978a,b). Also critical are additional research on limiting factors and increased emphasis on education, especially of rural peoples.

To be most effective, these management and conservation activities should be enacted on a regional basis. Luthin (1987), in discussing the conservation needs of storks, noted that a species' conservation concerns will often differ within its overall range. Also, because more than a single wading birds species may be dependent on regional resources, it is often within this multispecies context that management plans should be drafted. These plans, single-species or regional, are essential to define and guide conservation activity.

In some parts of the world, mankind is belatedly attempting to halt the destruction of forest and wetland habitat in which the majority of storks, ibises and spoonbills live. But it is not clear if it is too late for some populations.

Endangered means that a species or subspecies is in danger of extinction, and its survival is unlikely if the causal factors continue to operate (Collar and Stuart 1985). Populations that are decreasing may be

Figure 17. A Milky Stork flying over the nesting colony (northwestern Java, Indonesia).

considered vulnerable if further declines could make them endangered. Some species are vulnerable because of their rarity, which may or may not be due to human intervention.

We consider five species and two subspecies to be endangered, and six species to be vulnerable. These species encompass over 20% of the world's species of storks, ibises and spoonbills.

Amongst the storks, a number of species are endangered and many more are decreasing in numbers in some or all of the areas they inhabit (Luthin 1987, Collar and Andrew 1988). The Storm's Stork is a vulnerable species that has never been common and is seldom seen. Until recently we were not even sure of its status and so may never fully understand its biology before it becomes extinct. Other species are rare because of man, the Lesser Adjutant (vulnerable) and Greater Adjutant (endangered) Storks have all but disappeared over most of their range and are now in grave danger. The vulnerable Milky Stork remains secure only in the Indonesian archipelago. The Oriental White Stork and Black Stork, both vulnerable species, are increasingly confined to isolated breeding sites.

Ibises and spoonbills have a number of species at risk (Manry 1986). Of the six species of spoonbill, the Black-faced Spoonbill is the most endangered, having retreated as a breeding bird to a few islands off the North Korean coast or perhaps to other unknown sites yet to be discovered. The endangered Giant Ibis may just be hanging on in isolated areas in Cambodia and perhaps Vietnam. The endangered Davison's race of Black Ibis now occurs only in Vietnam and possibly Indonesia. The endangered Waldrapp Ibis has now gone from Turkey, appears to be rapidly decreasing in Morocco, and seems to be on the verge of becoming extinct (Hirsch pers. comm.). The highly endangered Oriental Crested Ibis is now known to occur in the wild only in Qinling Shan in south Shaanxi, China, where the known population is in the low dozens. The continued existence of the dwarf São Tomé Island race of the Olive Ibis has only recently been confirmed, but the situation is extremely precarious for this endangered race. The once widespread Madagascar Crested Ibis is vulnerable due to habitat changes that have been occurring in Madagascar.

Everywhere pressures of human population have affected even the widespread species, and as suitable environments shrink so the pressures on all species increase. Regional decreases in numbers are documented in most species for which such data are available. It is likely that in the last 50 years that populations of most storks, ibises and spoonbills have been reduced by at least a half, and in many species by more. The extent of these reductions vary regionally.

Bird populations in North America are probably the best

known in the world. Trend in numbers and distribution suggest that considerable changes in ranges and populations have been underway for many decades. Perhaps the greatest decreases are in the Florida Everglades, where once thriving populations of American Wood Storks and American White Ibises have been decreasing to the point of local extinction (Frohring et al. 1988). The desperate position of the Ciconiiformes has developed with great rapidity. On the other hand, these species still maintain sizable populations elsewhere in North America and into South America. Within the United States the conservation and management needs are becoming well recognized (J.F. Parnell et al. 1988), but many countries have not the resources available in the USA to fight for the survival of decreasing species.

Over much of South America, populations of all species remain high (or unknown). Even where historical decreases have occurred, there is evidence that populations may be returning. However in South America, apart from a few individuals and isolated concerned government or private bodies, conservation of habitat or species is not yet underway.

In Europe the protection of species by concerned government and private bodies is holding back the deterioration, but species such as the White and Black Storks are falling in numbers annually. Eurasian Spoonbills are confined to a few sites in western Europe. The former indifference, or active persecution, in western Europe has, except in Mediterranean regions, belatedly been replaced by a growing concern, manifesting itself into sometimes ineffective but now increasingly professional attempts to protect such species on their feeding and breeding grounds. Quite recently, however, it has become clear that in eastern Europe, pollution created by ill-conceived and inefficient industrialization is on a much larger scale than was previously realized. Some areas, it is thought, may never recover from the environmental damage, but all require attention.

In Africa, the picture is probably the most favourable as most species remain widespread and even common (Collar and Stuart 1985). North of the Sahara, the Waldrapp Ibis is fast on its way to extinction. It is well to note that such local extermination is not new in the area. The ancient Egyptians mummified Sacred Ibises by the hundreds of thousands, perhaps over a million, undoubtedly reducing the populations that probably were finally extirpated by land use changes (Goodman 1988). Modern times have produced oil spills and the catastrophic effects of recent wars have yet to be evaluated. Historically the peoples of subSaharan Africa have shown tolerance to creatures around them, but increases in human population have begun to change the face of this continent, and the need to feed increasing numbers

Figure 18. A Bald Ibis (northeastern South Africa).

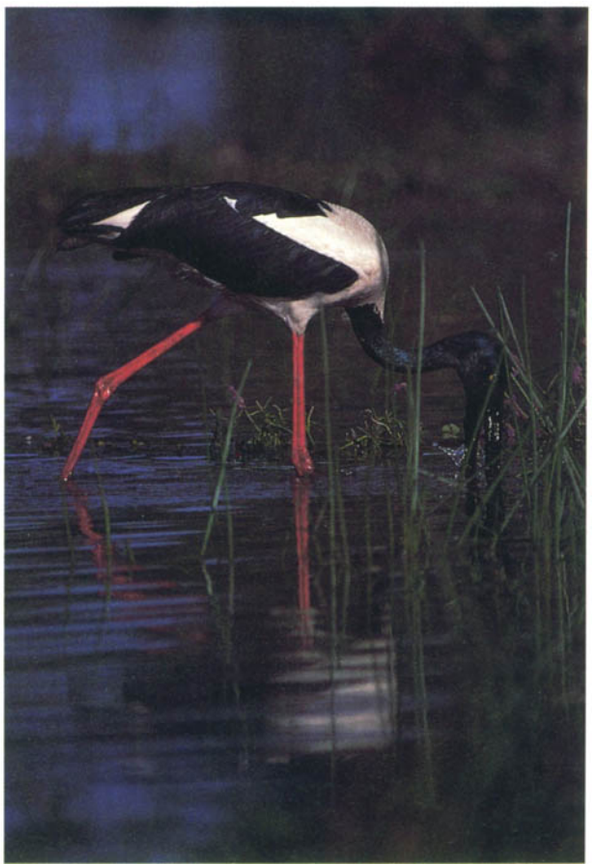
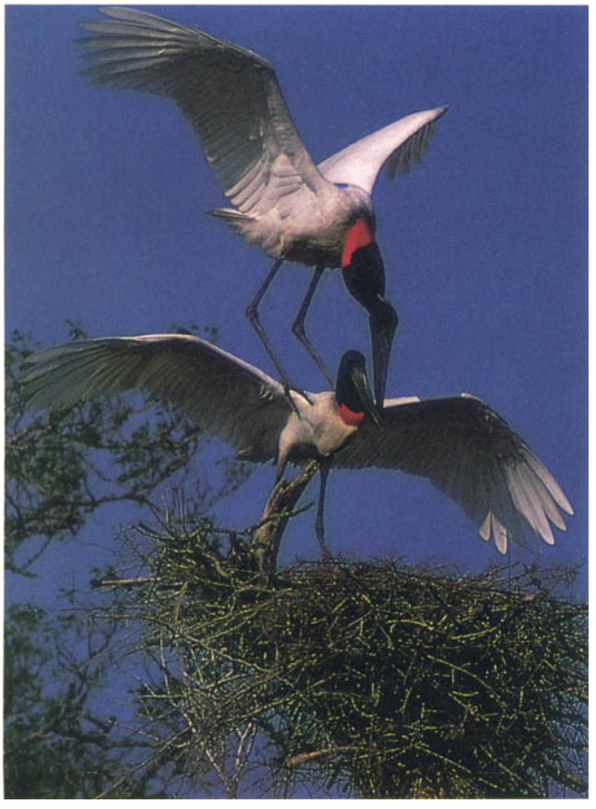


Figure 19. A female Blacknecked Stork foraging (northern Australia).



of people has, together with ill-conceived development schemes often funded by western agencies, put pressures on all species of storks, ibises and spoonbills (Collar and Stuart 1985). Island forms in the Atlantic and Indian Oceans continue to be at great risk.

In Asia the picture is very bad (Bain and Humphrey 1980, Hancock 1989). Here many wading bird species are very near extinction over much of their former range. Only in parts of India and in the, as yet, undeveloped areas of the Indonesian archipelago do some of the former abundant species survive in any numbers. The reasons for such a dramatic change, which has occurred since the end of the Second World War—a matter of about 45 years—are not hard to find. The elimination of endemic diseases and the resultant population explosion combined with a huge increase in the standard of living of many, though by no means all, its peoples have meant a rapid and urgent need to exploit all its natural resources (D.A. Scott and C.M. Poole 1989). Southern and eastern Asia comprises only 14% of the world's land surface, but support at the present time 56% of the world's human population. Furthermore this huge population is expanding at about the rate of 55 million per annum (D.A. Scott and C.M. Poole 1989).

Also in Asia, not only has continuous warfare in many areas destroyed much of the formerly unexploited natural habitat, but the demand for food under such circumstances has meant the killing of large birds for food. Weapons are now readily available for shooting, and in many areas no feeding bird is safe from the gun, and no breeding bird safe from the trap. There has been a breakdown in the traditional religious beliefs in some nations, notably China, such that temple grounds and monastries, which traditionally provided protection for storks and ibis colonies, now seldom do so today. An exception which still enjoys protection in the temple confines is the Asian Openbilled Stork of Thailand.

Today's awareness of the need for conservation measures has barely touched some nations or regions of Asia. The peoples of Pakistan, have a tradition of hunting which, using modern weapons, has served to nearly exterminate all the species of wading birds that bred in their land. War and poverty in the Philippines have brought with them heavy deterioration in the numbers of large birds. In Japan the recent stirring of conscience there has come too late in the day for most species.

The subcontinent of India provides, perhaps, the clearest example of how religious and traditional tolerance has meant the survival of storks, ibises and spoonbills, and other resident and migratory species of large water birds. In areas where such ancient customs either do not pertain or have been lost beneath the struggle to survive, such species have

Figure 20. Jabiru Storks at the beginning of a copulation, with neck-bands a fiery red (northeastern Argentina).

Figure 21. A female Saddlebill Stork at its nest with three nestlings about 45–50 days old (western Kenya).

been exterminated. An example is the Black Ibis, which has its stronghold in Gujarat, a state composed mainly of tolerant, strict Hindu peasants and landowners. Here this species is quite tame, feeding around village ponds and nesting near to houses and other occupied buildings. But in states where hunting and trapping are still carried out, it is only in the nature reserves that the Black Ibis survives. Even so, in Gujarat, such tolerance has not saved the Blacknecked Stork. Drought conditions have dried out wetlands, and increasing demand for firewood has resulted in the destruction of trees on a vast scale, so that this bird has lost its traditional nesting sites, with the result that no breeding pairs remain there.

Australia is the area of the world that retains its several species in greater abundance than perhaps any other. The Blacknecked Stork is at the southernmost limit of its range in Australia and New Guinea, having been almost totally wiped out in the rest of Asia apart from a few pockets of birds in India and perhaps Cambodia and Vietnam (Hancock 1989).

Conservationists and conservation organizations in India, Africa and Asia are struggling with the problems they face. Private organizations such as Interwader in Asia are surveying the shrinking wetlands and recommending methods of protecting them. The ICBP is donating funds for work in many parts of the world. Brehm Fond has sponsored surveys and workshops on colonial bird conservation in Asia.

In spite of all the measures being taken, there is an inevitability about the demise of some species. Given the need to preserve genetic stocks represented by these species and the hope that habitat restoration will allow reintroduction, it would seem likely that captive breeding remains the only hope in some cases. The Waldrapp Ibis thrives in captivity with some 500 birds, whereas in the wild the total population may well be below 100. The Oriental Crested Ibis numbers in China may be increased if a way can be found to breed them successfully in captivity. Many storks prosper under captive conditions and could be released in the wild if suitable protected areas can be found for them. The zoological parks of the world are attempting to breed these species, and such efforts should be encouraged (Luthin et al. 1986, R.E. Johnson et al. 1987a,b). Of course, all proposed reintroductions require detailed consideration and study (Kushlan 1980, Seward 1987).

The need for education is paramount to the success of any conservation measures. The recent discovery of the few colonies of Greater Adjutant Stork breeding in villages in Assam heightens the need in that area (Saikia and Bhattacharjee 1990) As a scavenger the species requires a food supply provided by man and his domestic animals, and does not appear to thrive in nature reserves where man is excluded. Conservationists, scientists, farmers and local landowners do not mix happily and readily together, and great care will be required if useful and productive understanding is to be reached in Assam, and indeed in many other areas where man, stork, ibis and spoonbill live in close proximity.

Similarly, in South America, education efforts must be aimed at both the populace and government agencies. Popular programmes, environmental education, and in country and out of country workshops for wildlife professionals may be used with success. Without such education, the best laid conservation scheme will come to naught.

Figure 22. White Storks copulating on a rooftop nest (southwestern Poland).

Courtship and Reproduction

In order to reproduce, storks, ibises and spoonbills must form pair-bonds, mate, build nests, lay, incubate and defend their eggs, and rear their young at least until the chicks are able to fly safely from the nest. Reproduction is a complicated affair, requiring in all these species the cooperation of both parents.

A few species, such as the Black Stork, and the Hadada, Spotbreasted, and Black Ibises, nest alone in pairs. These usually are found in tall trees, especially in forests. Most species nest in colonies. Colonial species may nest on the ground, in reeds or in trees, depending on the species and the environment. Perhaps the most unusual are those that nest on cliffs, including the Waldrapp, Bald, Wattled and Buffnecked Ibises.

Timing of nesting differs among species and locations. Both photoperiod and environmental conditions affecting food availability seem crucial in determining nesting timing. In the high latitudes, nesting is decidely seasonal and is associated with migrations out of the nesting area in the local winter. In the subtropics, nesting is often in the drying season. In the tropics, some species may nest nearly all year round. In all cases nesting occurs during the local period of high food availability. In times of low food availability, especially due to inappropriate rainfall or surface water conditions, nesting may be postponed or may be skipped in a given year. The Waldrapp and American White Ibises are examples (Smith 1970, Kushlan 1978b). The tight relationships of rainfall to nesting is particularly demonstrated in Australia, the Florida Everglades and Africa (Carrick 1962, Urban 1974b, Kushlan 1989a,b).

Meeting and overcoming environmental and social constraints on reproduction are achieved through the use of appropriate behaviours, some of which have been ritualized into displays that allow one bird to communicate with another.

THE PAIR-BOND

The pair-bond is the key to successful nesting. Both members of the pair participate in building and protecting the nest, incubating the eggs, and feeding and caring for the young until they fledge from the nest site under their own power. It seems that in these species a single parent is insufficient to supply simultaneously the protection and food needed to raise young.

Despite the importance to both individuals of maintaining a strong pair-bond to raise their young, it is becoming increasingly clear that promiscuous mating behaviour, called extrapair copulation, is extremely common in some species. Colonial nesting presents opportunities for promiscuity that are less available when, as in most species, birds nest in widely separated nesting sites within defended territories. The evolutionary advantage is clear: the promiscuous male increases its chance to sire additional offspring while the female is receiving a bold and clearly successful male who might father some of her young. But risks are also present, not the least of which is the potential loss of one's own nest or eggs if they are left unattended, as we have seen in the American White Ibis (Kushlan 1973b).

An important question is whether extrapair copulations result in insemination, and this is a difficult question to study in these birds. Another question is what are the strategies the male uses to defend its mate against such intrusions, while also attending to its other duties such as supplying nest building materials? In the Eurasian Spoonbill, most extrapair copulations occur while the resident male is away gathering nesting material; and, perhaps as a response, males usually copulate with their mate just

before leaving them to go on stick-collecting trips (Aguilera 1989, Aguilera and Alvarez 1989). Despite promiscuity, even if an intruder is caught in the act, the initial pair-bond usually persists, probably because the pair has little choice if they are to raise their young.

Pair-bonds last for at least a nesting episode. If nesting is interrupted at an early stage, many species can nest again during the same season. Individuals of some species may re-pair in successive years, or even remain paired year-round. The White Stork is famous for maintaining pair-bonds over many years. It and similar species are said to 'mate for life'. In most cases, they re-mate as long as they both return to their previous site at the right time. If not, new mates may be taken. Several species of tropical ibises and several storks, such as the Saddlebill, Blacknecked and Jabiru, are solitary, non-migratory, and may remain together throughout the year. These pairs may not require extensive courtship at the start of the next breeding season.

Pairs form during a courtship period in which both birds engage in a series of behaviours that help establish and then maintain the bond. The initial stages are crucial in that the birds have to overcome the tendency to exclude other birds nearby. That is, for much of the year, a bird tries to keep other birds at a comfortable distance, yet, when pairing, is faced with accepting the close proximity of another bird.

One correlate of pair formation in most species is a seasonal change in the colour of the bill, face, legs or other exposed skin, called the soft parts. In the American White Ibis, the face turns a bright red and the bill black, and the females develop a red gular pouch under the chin. In the Sacred Ibis, the skin along the breast and under the wings turns bright scarlet and is highly visible when the bird flaps its wings. The Sacred Ibis also develops ornamental plumes at this time. The Oriental Crested Ibis has a unique type of cosmetic coloration. It uses its head to paint its pinkish back feathers grey with a secretion from its preen gland. These colour changes enhance the displays of the birds.

The overall process is more similar between species of storks, ibises, and spoonbills than it is different. However, the details of the behaviours used in the process, called displays, differ among species. Species-specific courtship displays reduce the chances of mating with the wrong species. The occurrence of various displays and the different forms of display can serve as distinguishing characteristics between the species, just as morphological and plumage differences do.

Most of the displays shown by storks, ibises and spoonbills during their courtship are 'derived' activities (Tinbergen 1952). These are behaviour patterns—usually borrowed from one or more other activities such as preening, fighting or fleeing—that have evolved as social signals. Displays have become specialized through a process known as 'ritualization' (Blest 1961), in which the elements of the display have become elaborated and stereotyped into the species-specific patterns that are recognized by the recipient bird.

The various displays used by storks, ibises and spoonbills can be defined and categorized. Many of these behaviours have been previously described and named (Kahl 1966a, 1971f, 1972a-d, 1973b, 1983, 1988a). Displays are named according to their component body movements, without assigning or assuming motivation. For purposes of enhancing clarity, increasing descriptiveness and reducing motivational inferences, we have renamed some of the terms currently found in the literature. These changes are noted in the accompanying table.

So that the named ritualized behaviours will stand out and be easier to locate in the text, they have been capitalized. In general, using the same name for a behaviour in more than one species implies that the displays are homologous; that is, evolutionarily derived from a single display of a common ancestor. Certain displays show close similarities among the ibises and storks, and the herons (Hancock and Kushlan 1984). However, because of uncertainty as to the phylogenetic closeness of these groups, it is best to maintain a separate behavioural nomenclature, unless the similarities of the displays are so compelling as to lead us to imply their homology.

In general, the process of courtship starts when birds begin to gather near a potential nesting site during the daytime. Depending on the species, these sites may be patches of trees, marsh reeds, or cliffs. In most cases the nesting sites are characterized by some degree of remoteness or inaccessibility, and many are located on islands. In these

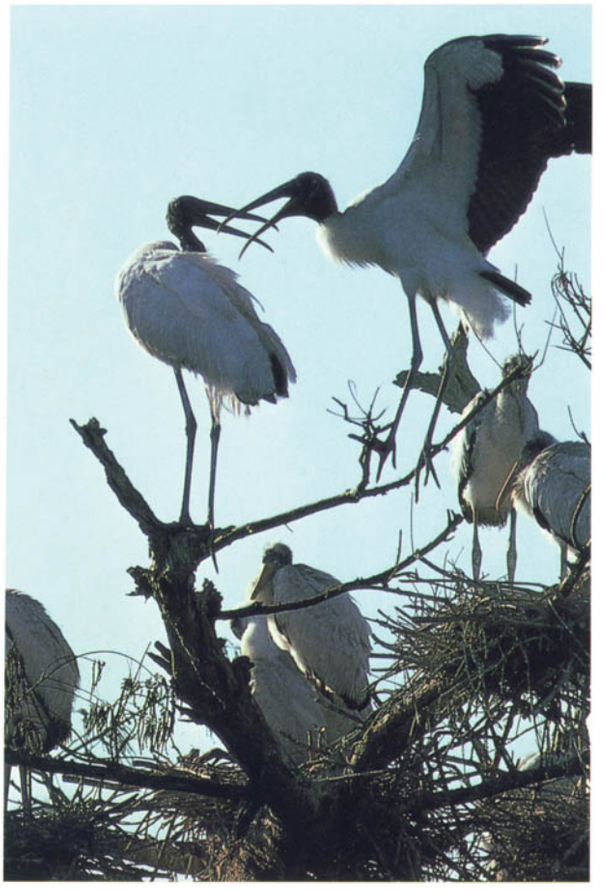


Figure 23. American Wood Stork. Social interactions between birds in a treetop colony (southeastern USA).

Figure 24. A Yellowbilled Stork feeding by tactolocation with bill held open and moved slowly about in water (central Kenya).

Figure 25. A Painted Stork sunning in the 'delta-wing' posture (northern India).

locations males behave in ways that serve to attract females and to advertise their readiness to mate.

Most information available is on colonial species, and generalizations are often based on these species. It can be expected that solitary species may have slightly different approaches to mate attraction. In some non-colonial species, individuals remain on an activity area year-round and may return to the same nest-site in succeeding years. The Hadada Ibis appears to exhibit pair-bonding behaviour even within a flock, as pairs of birds separate out to preen mutually.

In colonial species, the male birds stand in groups in a potential colony site and periodically fly about. The colony forms as displaying males and interested females gravitate toward each other, forming 'bachelor parties'. It is usual to find that a large colony is composed of smaller groups in which all the pairs are in the same stage of nesting, as a result of displaying birds having been attracted to each other.

A male eventually selects a display perch within the selected colony site in a location where he is visible to interested females. In most species the eventual nest-site is located at or near the display perch, so it is possible that the quality of the site a male is able to secure and hold against competing males may be of considerable importance in formation of the pair. Mate choice is primarily a matter of the female selecting from among available, displaying males.

The displays of the male also serve to intimidate nearby competing males. When the defensive content of a display is insufficient, fights can develop among males. The female approaching its chosen male also has to overcome his aggressive tendencies, and some of her displays at this time can be interpreted as appeasements. In the American White Ibis, the much smaller female can become quite bloodied during the process of gaining access to the male's defended display site.

After mate selection is made, the pairing is reinforced by additional displays that often continue for several days. These eventually lead to copulation. Since the displays leading up to pair formation and copulation are defined differently for the two groups (storks, and spoonbills and ibises), it is worthwhile to describe these separately.

COURTSHIP IN STORKS

In all species, courtship begins with a male making himself conspicuous and available to an interested female. In many situations, the male just stands conspicuously. During Standing, a bird may try to look imposing. The Marabou blows up its gular air sac.

One of the first active advertising displays used by male storks of the genus *Mycteria* in their bachelor parties or on their display sites is Display Preening, in which the bird repeatedly goes through the motions of running its bill down the primaries (the main flight feathers) of one wing then the other. It does this just as if preening, but the feather itself is not grasped, and perhaps not touched at all.

Often occurring during episodes of Display Preening,

Swaying Twig-Grasping display is executed by the male bending forward to one side and grasping a twig. Upon releasing the twig, the bird sways to the other side and repeats the process. A similar advertising behaviour found only in the openbills is the Advertising Sway. With bill gaping, the bird bends its head to its feet and lifts its wings slightly away from its body, while shifting its weight from foot to foot and swinging its bill from side to side.

The Head-shaking Crouch, is given by storks of the genus *Ciconia*, when a female approaches a displaying male. He inclines his body forward with head and bill low, wings slightly away from body and, while shifting from foot to foot, shakes his head in a 'no' motion, sometimes lowering the body to the nest in the process.

A ritualized response to disturbance is the Arching Display, given by all stork species. In this 'anxiety' display, the bird, from an erect posture with feathers sleeked down, leans forward and looks at the offending object. In some species this may be accompanied by spread wings and vocalization.

The generalized agonistic display among storks is the Forward Display. With the neck retracted, body horizontal, and feathers erect, the bird points its bill at its opponent and moves toward him. An antagonistic bird may also rattle its bill in a Forward Clattering Display. Although ritualized, these threat displays can lead to overt fighting should the intruder not choose to retreat. A hostile bird may pursue an opponent into the air using an Aerial Clattering Display. The pursuing bird flies after and above the opponent with its neck extended and bill pointed toward him. The attacking bird may clatter its bill but usually does not try to bite the opponent, who usually takes evasive action.

An intriguing, apparently agonistic, display is called Mock Fighting. On or near the nest-site, a bird suddenly erects its neck feathers and makes lunging grabs into the air as if fighting or catching a flying insect. The bird frequently loses its balance and has to flap its wings to stay on the perch.

The usual subordinate display of storks, is called the Upright Display. The submissive bird stands erect with head extended upwards, feathers compressed, and turns away from the threatening bird. At least two appeasement displays are used by the female stork in attempting to gain access to the male's courtship station, Balancing Posture and Gaping. Upon approaching the male, the female (of some species) assumes the Balancing Posture, holding her head low with her wings spread. This may be accompanied by bill Gaping, as if overheated, but the bird does not actually pant. As time passes without being driven away, she may close her wings but often continues to Gape with her head bowed.

Soon after acceptance of a mate, a male *Mycteria* may engage in a Flying Around Display. He takes off from the nest and flies in a tight circle before returning to land next to his mate.

Also during or soon after pair-formation, Bill Snaps become common. This behaviour, shown by both sexes in some species, involves a quick lift of the head to bring the bill to slightly above horizontal, followed by a snap of the bill. The display is used when levels of hostility are still high among the newly paired birds. A stork may infrequently give a bill snap when taking flight. During this display, the Pre-flight Snap, the bird bends forward and low, swinging its head between the legs. It then gives a single loud snap with its bill followed by a normal take off. Another display given before flight is the Erect Gape. The bird stands erect, with neck extended almost vertically and bill held slightly below the horizontal. Sometimes a low call is given. The Erect Gape may also be followed by a Bill Snap.

The Flap–Dash display—probably derived from foraging

Figure 26. Asian Openbill Stork. The Up–Down Display at a nest with large young (south-central Thailand).

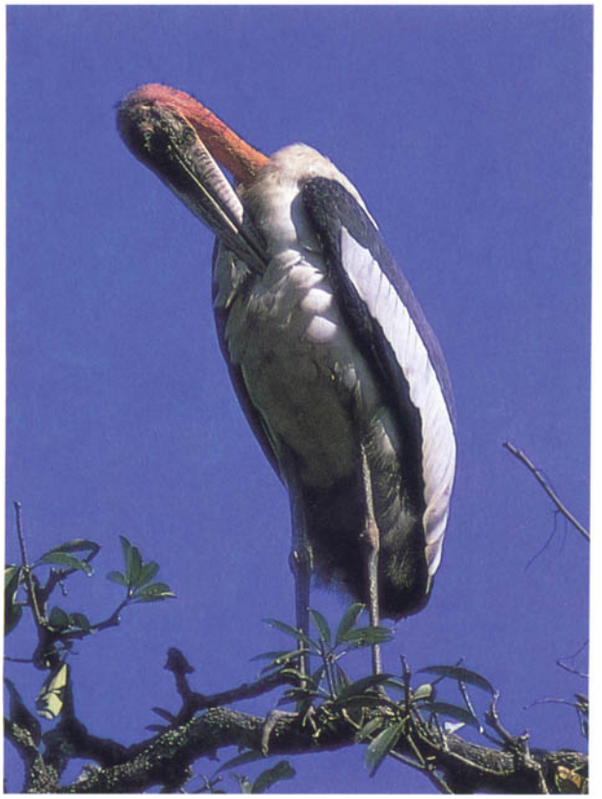


Figure 27. A female Greater Adjutant Stork preening near her nest (northeastern India).

behaviours—is performed on the ground or in shallow water by the Saddlebill, Blacknecked and Jabiru Storks. A bird, usually the male, flapping its wings, runs several metres away from its companion and then runs back again.

Following pair-formation, mates greet each other with an Up–Down Display, which is performed by all storks but differs among species. In the openbills and wood storks, the bird lifts its head vertically, and, with its bill gaping, it may utter short hissing or grunting vocalizations, while lowering the bill toward the floor of the nest-platform. Depending on species, during the head-up part of the display, the bird may snap the bill once or twice or repeatedly, or it may not snap its bill at all. In the Blacknecked Stork, the bill is not raised, but the wings are spread and fluttered and the bill is clattered rapidly. Other species show varying degrees of head movements and clattering during the Up–Down. The most extreme is reached in the White and Oriental White Storks, in which the head is thrown all the way back toward the tail and the bill-clattering is loud and prolonged. This is, perhaps, one of the most widely known of all stork behaviours. Up–Down Displays continue throughout the nesting season.

Copulation occurs at or near the nest-site with no pre-copulatory display. Characteristic of storks is for the male to clatter its bill or rattle it against that of the female during copulation. In storks, this behaviour is called Copulation Clattering.

A Nest-Covering Display has been observed in several species. The parent bird hides its eggs or young under partially opened wings.

COURTSHIP IN IBISES AND SPOONBILLS

The courtship displays are more poorly known among ibises and spoonbills than in storks. Many species have never been studied at all. None the less, from the information available, a number of displays can be identified. Certainly, additional studies on these species are needed.

As in storks, the males of colonial ibis and spoonbill species, and those that must pair each year, display for females. Upon choosing a display site, ibises and spoonbills tend to remain on it almost continuously. In fact, Display Standing may be considered the initial display in courtship. Display Standing can develop into Display Sleeping. In imitation of sleeping, the bird places its bill under its back feathers, although its eyes remain open. This behaviour appears to be quite contagious among neighbouring birds. It also occurs as a pause in active display, serving no doubt to maintain a bird's continued claim to a display- or nest-site.

Species that remain paired throughout the year perform displays that serve to reinforce the pair bond, and perhaps to coordinate breeding readiness. Pairs display together with simple behaviours such as Standing, Head-Shaking, Stick-Shaking and allopreening.

Ibises can be quite noisy when nesting, even those that are rather silent for most of the year. Calls differ among species from whistles to caws; they also may make noise with their wings when landing, taking off or flying around. Ibises and spoonbills use calls for contact, to communicate with mates, during copulation, and in agonistic situations. Some species, such as the Barefaced Ibis, perform duets (Luthin 1983a).

The active solicitation behaviour of unmated males, in species so far studied, consists primarily of three displays: Display Preening (Front and Rear), Display Shaking, and Bill Popping. Display Preen (Front) and Display Preen (Rear) occur when the bird appears to use its bill-tip to preen its primary feathers (Front) or to preen over and behind the wings (Rear). The Display Shake is given by a bird standing erect and holding its wings loosely. It then shakes the wings alternately up and down. The Bill Popping display occurs as the bird snaps its gaped bill shut, usually without sound, although at times accompanied by a quiet pop. In African Spoonbills, this display is given as the bill is raised to the horizontal or slightly above. In the ibises so far studied, it is given with the head extended and bill downward. Ibises sometimes also grasp a twig and shake it briefly. Bill Popping is very reminiscent of the Snap Display of herons and also is reminiscent of the Bill Snap of storks.

The solicitation displays may be given in any direction, not necessarily in the direction of a female, and sometimes toward neighbouring pairs. In some ibises, Bill Popping may be truncated into a more moderate form in which the neck is not extended. In ibises so far studied, the three

displays are often used together but not in any standard sequence. In the African, Royal and Yellowbilled Spoonbills, these three displays are given in succession: Display Shake/Display Preen/Bill Popping.

Another display, observed primarily in courting female spoonbills, is the Display Flight. The bird takes to the air, flying in a low circle or even a figure-of-eight while calling. It then lands near its point of origin, which is usually near an unmated male. This display is similar to the Flying Around of the storks.

The initial phase of pair-formation involves considerable aggressiveness by the male toward the intruding female. As a result, many of the initial behaviour patterns of courting male ibises and spoonbills have components of aggression or fear. When a bird is alarmed, the Erect Posture is assumed. The bird stands upright, feathers sleeked, bill down, peering at the disturbing object. This behaviour is similar to the Arching display of storks and may precede, but does not necessarily lead to, escape behaviour.

The basic aggressive behaviour of ibises and spoonbills is the Sparring Display, in which the bird assumes a horizontal posture and moves toward or lunges at an intruder using a bill thrust. The Sparring bill thrust may or may not make contact. An overt fight may follow. Two birds engaged in ritualized Sparring hold their feathers erect and bills gaped, while each reaches forward and snaps its bill towards the antagonist; it does not actually make contact. This behaviour is returned by the opponent, also without contact, and a stab-and-counterstab Sparring match commences, with birds alternating ritualized attacks. The aerial modification of Sparring is the Supplanting display, in which a bird flies at another bird, with its neck extended and bill gaped. The attacker slows its flight with its wings, and attempts to land on the opponent or, more likely, on the perch vacated by the displaced victim.

One of the most common activities of some species of ibises is appearing to rub their head on their back. The Head Rub is ritualized into a mutual appeasement display and also an advertising display. The bird places the side of its head on its shoulders, bill pointing upwards. The bird may then turn it slightly to vertical or even to the horizontal on the other side, in the rubbing motion, or it may make only a quick touch of the nape to the upper back. The female ibis uses this display prior to attempting to enter the male's display area, and the male may use it with other attraction displays. The origin of this display is clearly the similar comfort movement. In some species it is reminiscent of aspects of the Up–Down display of storks. In its vertical form, it is similar to the Stretch Display of herons.

Upon actually attempting to enter the male's display area, the female assumes a Bowing Display, in which she approaches the male keeping her body and head low, feathers sleeked back. She turns her head away from the

Figure 28. Asian Openbill Storks. High water levels prevented breeding at Bharatpur, India.

male, exposing the side of her head to him. The male generally reponds with a Sparring display and even an overt attack, in response to which the female may flee but does not fight back. The male responds initially by aggressive actions and eventually by acceptance of the female at the nest-site. This behaviour is identical in function and similar in appearance to the stork's Balancing Posture, except that the wings are not opened.

The aggressive phase of pair-formation ends as the male accepts a female. Bowing Displays continue, and when one of the pair returns to the nest, a Greeting display is given. With head feathers erect (if present) and bill gaped upwards, the bird calls and may flap its wings. In spoonbills the Greeting is given with the bill upward, whereas in ibises the head and bill are slowly brought downward to the vertical in a bowing motion, before the vocalization. Especially in spoonbills the downward component is recognizable as a distinct display, Head Shaking. Bending forward simultaneously with bills downward and closed, the birds shake their heads in a 'no' motion while lowering them to the nest. Some ibises also Head Shake. The birds' necks may overlap, the taller male usually being on the top. The Greeting displays appear similar to the Up–Down of storks.

Stick Shaking may also occur. Bending forward with bills pointed down, the birds grasp nest material and shake their heads rapidly from side to side. Again, necks may cross and overlap, with the male on top. This behaviour is similar to Head Shaking, except for the involvement of twigs.

Another mutual display of paired birds is the Head Quiver. Standing upright with head feathers erect, a bird twitches its head several times. Generally the display is performed by both sexes in succession or simultaneously.

Following the acceptance of a mate, pair-formation is completed through copulation. Allopreening continues as do Head Shaking and other Greetings. During the Copulation Display, the male climbs on the back of the nearly horizontal female, and brings his cloaca into contact with hers, while flapping his wings for balance. In the process, the male may also perform a bill-shaking behaviour in which he grasps the female's head or bill or holds his bill alongside her neck while he shakes his head or nibbles at her feathers.

A later defensive posture is the Nest-covering Display. A parent bird erects its feathers, orients toward the threat, and droops its wings down and over the nest. This display is clearly homologous to the behaviour of the same name in storks.

Birds of a pair often engage in preening each other (allopreening). They especially nibble the feathers of the partners head and neck. Throughout nesting the birds commonly occupy themselves with preening, head-rubbing and shaking. Although these are functional maintenance behaviours, they probably also serve a display purpose, helping to maintain the pair-bond.

Figure 29. A Eurasian Spoonbill with well grown young (Bharatpur, India).

Figure 30. Young Asian Openbill Storks leave the nest early (Bharatpur, India).

NESTING

After courtship and pair-formation, nesting begins. Depending on the species and the habitat, nests may be made out of sticks, reeds or vines, often with green material added. Nest-building is generally the province of both sexes. The male is largely responsible for gathering the sticks. The female accepts the material. The sticks are then inserted by the female into the developing nest bowl by a behaviour called 'tremble-shoving', holding the stick by an end and wiggling it into the nest matrix. Behaviours during nest-building and maintenance may involve the real or feigned picking, grasping or presenting twigs to the female.

At this time, appeasement and pair-formation displays become less frequent and less intense. The eggs are laid a day or more apart, and incubation usually begins with the first or second egg. The members of the pair alternate incubation duties. The larger male is often in attendance at the nest for much of the day.

Young hatch asynchronously and are unable to stand from the first ('altricial young'). The bills of hatchlings are short, straight and rounded, even in ibises and spoonbills. The typical shapes begin to develop soon thereafter.

Young are fed by both adults on regurgitated food. Storks regurgitate food onto the floor of the nest and their nestlings pick it up, whereas nestling ibises and spoonbills insert their entire head and bill down the parent's gullet to receive food. During the first few weeks after hatching, one adult remains at the nest at all times, as the parents alternate foraging trips. Storks also bring water to nestlings.

When the young are further developed, both adults leave the nest to forage at the same time. Nestlings respond to disturbance with threat and alarm displays. Storks respond with a Nestling Bristle and may give Forward Displays. Ibises and spoonbills assume an Erect Posture.

Nestlings solicit food from their parents using a Begging Display. Facing the parent while resting on its tarsi, the nestling raises its head and bill, bobs them up and down, flaps its wings, and gives a begging call. As the nestlings grow they may give the display while standing or—especially in the case of the smaller, more active ibises and spoonbills—while running or even flying after the parent. Larger young may catch their parent, and placing a wing over the parent's shoulder, pin him or her down while they force feed from the gullet.

Large young spend considerable time flapping their wings. In some colonial species, it appears that young leave their nests to form groups, called crèches. The young can fly long before they depart from the colony. They usually return to near their nests to be fed by the parents, which they appear to recognize by call and sight. Fledging periods vary widely, according to the size of the species, from less than a

Figure 31. Storm's Stork. A unique photo of an adult standing on an active nest; only two nests of this species have ever been found (in Thailand and Sumatra). Photo by courtesy of the late Seub Nakhasathien.

Figure 32. An Asian Openbill Stork in Bharatpur, India.

month in the smaller ibises to more than 3 months in the larger storks.

Although for most species, parental care ends soon after fledging, the young of some species of ibises—those that appear to maintain long-term pair-bonds—continue to use the family's home range for a time, and are even fed there by the parents.

Changes to display names

	Original name	New name
Storks[1]	Forward Threat	Forward Display
	Aerial Clattering Threat	Aerial Clattering
	Forward Clattering Threat	Forward Clattering
	Snap Display	Bill Snap
	Anxiety Stretch	Arching Display
	Nestling Defence Display	Nestling Bristle
Spoonbills and ibises[2]	Alarm Posture	Erect Posture
	Appeasement Display	Bowing Display
	Flight Intention	Pre-flight Tipping

[1] Used in Kahl 1966a, 1972a–d, 1973b.
[2] Used in Kahl 1983, 1988a.

Figure 33. A captive Oriental White Stork at Vogel Park, Walsrode, Germany.

Figure 34. African Spoonbills Sparring and nest building on a rocky island on Lake Turkana, Kenya.

Feeding Behaviour and Ecology

Storks, ibises and spoonbills are among the more typical of the 'wading' birds, species that characteristically feed while walking about in shallow water. How these birds behave while feeding and what they can catch to eat are constrained by a general adaptive plan, millions of years old. That design includes long legs, long necks and long bills, all adaptations for feeding while walking through shallow water.

Because of this body plan, most species of storks, ibises, and spoonbills are highly aquatic, characteristically occurring in and around shallow water. The wood storks and the openbill storks epitomize a near total dependency on water and are found only in very specific types of aquatic habitats. However, most species can also feed on land should compelling suitable food become available there. Some, such as Abdim's Stork and the Waldrapp, Bald and Hadada Ibises, are more terrestrial than aquatic. They feed mostly on insects in dry grasslands and farm fields. Yet they retain the primordial body design, modified by somewhat shorter legs, necks and bills.

All species are both liberated by and constrained by their wading bird heritage. Indeed, it is instructive in understanding the ecology of these species to consider what foraging opportunities can be possible for large birds built according to these general specifications.

The various behaviours used by storks, ibises, and spoonbills in their foraging activities can be delineated and defined (Kushlan 1978a). Recognizable similarities in most behaviours among the species allow use of the same terminology in both families. In this book we capitalize the named feeding behaviours in order to allow the reader to identify them in text. We also capitalize, as is the custom, courtship behaviours. However, unlike courtship behaviours, most feeding activities are not ritualized displays.

The number of behaviours identified as being used in feeding is surprisingly extensive. No species is known to feed in all the ways so far documented. Some species do exhibit quite a variety. The Roseate Spoonbill, for example, has been documented as being able to use eight different feeding techniques.

The most universal feeding behaviour is Standing. That is, a bird simply stands in one place and captures prey as it is encountered. Standing can be used on land or in the water, or even while mobile—African Openbill Storks Stand on the backs of moving hippos (Kahl 1971c). Typically, Standing foraging involves capturing prey that is on the ground or in the water. Two special types of Standing behaviour have been recognized when prey occur other than in the water. When Standing Flycatching, a stationary bird catches prey that is airborne. When Gleaning, a Standing bird catches prey that is on an emergent plant or some other above-water object. Another variation, which occurs while Standing, is Flipping. A bird turns over an object to catch what is underneath. In Foot Stirring, a bird vibrates its foot or leg, to stir up potential prey.

No species, or even an individual, forages solely by Standing, because prey-capturing opportunities are soon depleted at most feeding sites. To move from place to place, birds intersperse Standing with more mobile behaviours. The most widespread behaviour is Walking Slowly, in which a bird walks or wades at slow speed usually continuing to seek prey. Faster passage is achieved by Walking Quickly and by Running. Walking Slowly can be recognized by the bird's slow rate of progress, as slow as a step or two per second. Running, on the other hand, can be recognized by its rapid rate of progress, such that the bird occasionally needs to use its wings for balance. Of course, these classifications are relative and not totally distinctive.

The relative amount of Standing and Walking depends on the species and the situation. The Shoebill typically Stands in one place for long periods at a time, whereas ibises and spoonbills seem always on the move.

The usual prey-capturing technique involves a Bill Grab in which the bill grasps a prey item, using the mandibles as pincers. Unlike herons, which strike from a recoiled neck (Hancock and Kushlan 1984), storks and ibises Grab prey without a darting stroke. The Shoebill is unusual in that its Grab is accompanied by a Body Lunge, in which the head and trunk are thrown at the prey. The bird often ends up partially submerged (Guillet 1979). Some food can be captured in a more leisurely manner by Pecking. A bird simply uses its bill to pick up an item from the water or substrate. Wood storks use a highly specialized prey capturing behaviour, the Bill-snap Reflex. Upon contact between a prey item and the open bill, the two mandibles close reflexively at a speed averaging 25 ms in the American Wood Stork (Kahl and Peacock 1963).

Several special techniques have developed to allow birds to forage without using their eyes. The most widespread is Probing, in which a bird quickly and repeatedly moves its bill tip into and out of the water or substrate. This is the characteristic non-visual foraging method of ibises, which have innervated bill tips that register contact with a prey item. It is also used by many storks, including openbills, typical storks and giant storks. In ibises several types of Probing have been distinguished according to water depth and rapidity of the probe (Kushlan 1977a). One can recognize Shallow Probing (the bill is inserted fewer than 2 cm into the substrate), Deep Probing, Standing Probing, Walking Probing and Multi-probing (Walking interrupted by Standing Probing). Groping is a similar behaviour in which a bird places and moves its open bill about in the water. It is the characteristic component of the feeding repertoire of the wood storks.

Head Sweeping (Head Swinging of Kushlan 1978a; Slow Sweeping of Vestjens 1975b) is the typical tactile feeding behaviour of spoonbills but is also used by ibises. Vestjens (1975b) showed that the details of Head Sweeping differed in the two Australian spoonbills. It is usually accomplished while Walking Slowly. When performed while standing still and searching a site with short sweeps, it is called Intensive Sweeping. Forward Ploughing takes place when a bird walks with its bill under water and projecting forward, rather than swinging it sideways. Dragging is similar except that the bill is dragged through the water at the bird's side.

Wings are also used during foraging. Feeding while actually in flight has not been recorded in storks, ibises or spoonbills, although it can be common in some species of herons. Feeding birds do take short repositioning flights, however. In Hopping, a bird flies up and alights nearby, even adjacent to its former feeding spot. In Wing Flicking, a bird quickly partially extends and retracts its wing; whereas in Openwing Feeding, a bird completely extends and retracts one wing at a time. These behaviours appear to serve to frighten prey, especially fishes, into movement.

Several behaviours tend to be strung together in various ways to create a feeding sequence. The wood storks, for example, typically forage by alternating Standing with

Figure 35. Immature Painted Stork (Bharatpur, India).

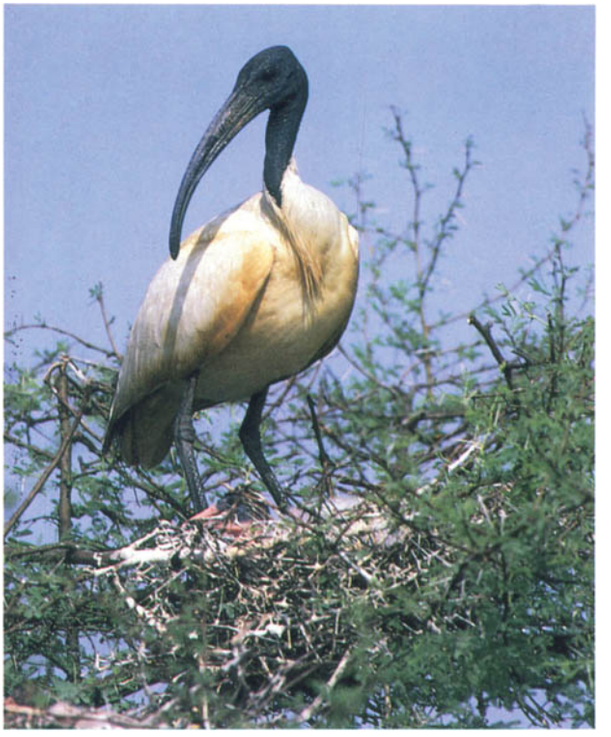


Figure 36. An Oriental White Ibis at Bharatpur, India.

Figure 37. African Openbill Storks feeding on snails in a lily pond (Tana River, Kenya).

Walking Slowly, while Groping with their open bill and Foot Stirring. At the same time they Wing Flick or Openwing Feed on the same side as Foot Stirring. The mix of these actions increase the activity of potential prey, and therefore the chances of its swimming into the bird's Groping bill (Kahl 1964, 1972b).

The Blacknecked and Saddlebill storks Walk Slowly or Run while Probing vertically in the water with each step. The American White Ibis is typical of a bird with less restricted sequencing (Kushlan 1977a). It will Walk Slowly while Probing; then, stopping at the edge of the water it may Peck at the mud surface or attempt to excavate a crayfish from its burrow by Standing Deep Probing. It then might move to deep water where it will Head Swing like a spoonbill.

Once a bird captures a prey item, it must be 'handled'. Small prey can be consumed immediately. Ibises can swallow such items nearly instantaneously by closing their bill tips while slightly pushing their head forward. Large prey have to be softened or broken into smaller pieces. A large food item, dead or alive, can be handled by Biting (i.e. mandibulating the prey) or by Stabbing (i.e. repeatedly poking and piercing it with the bill). The Australian White Ibis holds mussels against a rock with its feet whilst stabbing them with its bill. Handling time goes up exponentially as prey size increases, soon reaching impractical limits such that a bird might forgo eating a captured prey item in favour of resuming the search for a new one (Kushlan 1979c).

Divergence among the several lineages of storks, ibises and spoonbills is reflected, indeed in large part influenced, by their feeding behaviours and accompanying morphological features. One major evolutionary and ecological division is among species that feed primarily visually, by seeing their prospective prey before catching it, and species that feed primarily tactilely, by feeling prospective prey with their bill (Kushlan 1978a). It has been shown that the American Wood Stork feeds just as effectively without use of its eyes as with them (Kahl 1964). The primarily visual foragers, including the typical storks and adjutants, generally Grab the prey items they see. The primarily tactile foragers, including the ibises, wood storks, openbills and spoonbills, typically use Probing, Groping and Head Sweeping. Despite these overall adaptive trends, most species have the flexibility to use both visual and tactile methods when the appropriate occasion presents itself.

Given the correlations between feeding behaviour and morphology, much of the feeding story of each species can be told by examining their primary feeding apparatus, their bill. The divergence between ibises and spoonbills is essentially one of billshape. The ibises have thin downturned bills

Figure 38. A Hadada Ibis feeding in Kenya.

Figure 39. A Buff-necked Ibis in Argentina, South America.

whereas the spoonbills have straighter, flattened bills, each representing a basic morphological type for tactile aquatic foraging. Ibises that feed in terrestrial habitats, such as the Green Ibis, have shorter bills than those that feed in water, such as the American White Ibis.

The storks have an even greater diversity of billshapes. Ranging from the enormous Grabbing bill of the Jabiru Stork, to the specialized bills of the openbill storks and the Shoebill. Openbill storks probe for snails, capturing and opening them in their bill-tips. The Shoebill feeds visually, Grabbing its very large prey. The wood storks have slightly down turned bills, reminiscent of the ibises.

Another peculiar morphological correlation with feeding behaviour is the colour of the feet of the American Wood Stork. Its feet are pinkish, contrasting with its darkish legs. This colour possibly serves to enhance the effectiveness of Foot Stirring while feeding.

Some species are solitary foragers. They often use simple feeding behaviours such as Standing or Walking Slowly, stalking prey in ways that are not enhanced by a crowd. The Shoebill is the archetypical example of a solitary species. Others are solitary at one time of year and more social at another. The Spotbreasted and Hadada Ibises are two examples of species that nest solitarily but feed in groups when not breeding.

The great majority of species are capable of feeding in the company of other birds. Generally speaking most storks, ibises and spoonbills feed at least some of the time in social associations, called feeding aggregations, which form at sites of high food availability. Others show the higher level social organization typical of flocking.

A correlation between nesting and feeding dispersion is too great to be a coincidence. Colonial nesting and communal roosting provide exceptional opportunities for feeding together (Krebs 1978). Birds nesting in the same place can take advantage of foraging opportunities found by other birds in a process called social facilitation. Either by following birds flying to the feeding grounds or by seeing other birds feeding, wading birds are able to identify promising feeding sites and join the aggregation of foraging birds assembled there.

Many of the communally foraging species are white, a colour that has been demonstrated to attract wading birds to a feeding site (Kushlan 1977e). This raises an interesting question: once a bird finds a profitable foraging site, why should it advertise the place to other birds? At least two non-exclusive possibilities present themselves. The first relates to the character of the feeding sites used by most of these species. These sites, such as drying ponds and shallow wetlands, are ephemeral in that they are suitable for feeding only for short periods. Also in such cases the amount of food present is more than one bird can eat in the short time it will be available. Thus there may be no harm in inviting other birds to join the feast. The second possibility is that a foraging bird actually benefits from having more birds at its feeding site. One benefit may be in hiding from predators within a large aggregation of other birds. More directly, the prey present are disturbed by the feeding activity, which increases the probability of one bumping into a waiting bill.

This is a form of mutualism, a form of interaction between individuals or species from which both benefit. A number of instances of commensalism (an interaction in which one animal benefits and the other is unaffected) have also been reported in storks, ibises and spoonbills. Generally a visually foraging species follows a tactilely foraging species, benefiting from the prey the latter stirs up (Kushlan 1978a).

The subtle interactions among species, as noted above, may have lead to the social signalling function of the white plumage found in many species of storks, ibises and spoonbills (Kushlan 1978a).

Feeding aggregations also include other aquatic birds, especially herons and cormorants, though aggregative foraging carries with it certain risks, especially that of losing a captured prey item to a robber. Small birds can fly over and snatch a prey item from the bill of an ibis or stork. Larger wading birds also steal from smaller wading birds (Kushlan 1978c, Kushlan et al. 1985). Especially at risk are prey that take time for handling.

Some species that feed in family groups may tend to feed in more permanently available feeding sites. Species that remain in family groups, represented by the Blacknecked and Saddlebill storks and several species of ibises, also use the same foraging area for large portions of the year. Members of the pair forage within sight or hearing of one another but only join aggregations if one happens to form in their home range.

Most storks, ibises and spoonbills feed primarily during daylight. However, some—especially among the tactile feeders—will forage at night, and even visual feeders can secure prey on bright moonlit nights. In general, the smaller species begin feeding at sunrise. Storks often do not leave the colony site for feeding grounds until later in the day. This is because they travel long distances, not by flapping flight, but by soaring high on thermals and then gliding a long way to the next thermal. Such species leave the colony or roost when the ground heats up in mid-morning, forming the thermals. In certain species, such as the American Wood Stork, some individuals may spend the night at the foraging ground, returning to the colony the next morning (Kahl 1964). Outside the nesting season, storks, ibises and spoonbills spend much of the middle of the day resting near the feeding ground.

Storks, ibises and spoonbills are overwhelmingly carnivorous, each species eating various sorts of fish and amphibians, snails, crustaceans, insects and other aquatic invertebrates. The bulk of the diet of a population may consist of very few species of prey.

The most specialized group is the openbill storks, whose peculiar bill allows them to extract aquatic snails from their shells (Kahl 1971c). Thus snails make up almost all of their diet. With their Probing bill, ibises are especially adept at capturing small invertebrates, such as prawns, crayfish and aquatic insect larvae that live on the bottom or on aquatic plants. Similarly, they can probe into loose soil or grass to extract terrestrial insects and their larva. Faster-swimming

Figure 40. White Storks feeding on drained carp ponds in Israel.