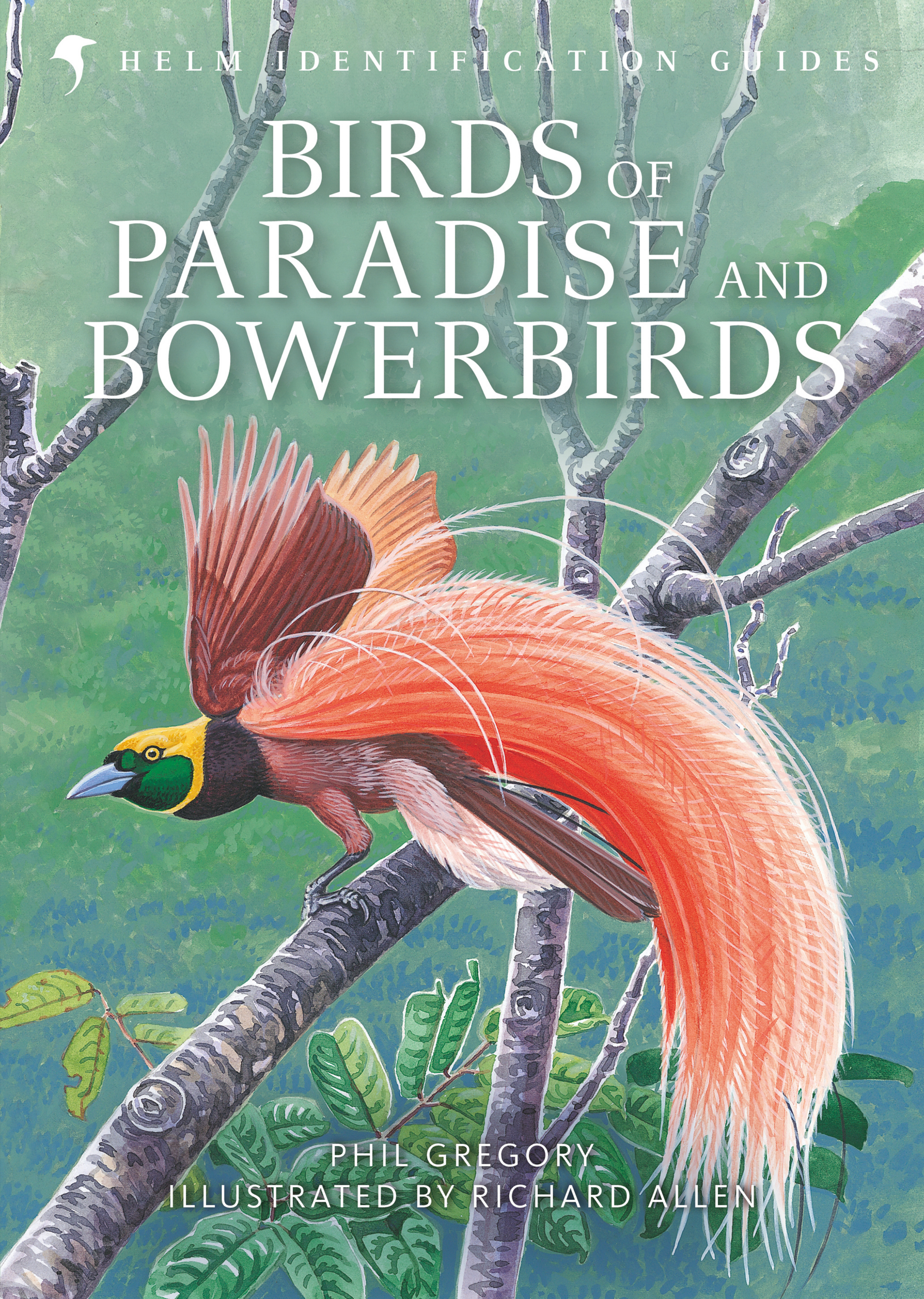
HELM IDENTIFICATION GUIDES

# BIRDS OF PARADISE AND BOWERBIRDS

PHIL GREGORY

ILLUSTRATED BY RICHARD ALLEN



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Phil Gregory

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Dedicated to the memory of Ian Burrows, instigator of the project and sadly missed.

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| Obi Paradise-crow | *L. (p.) obiensis* | Bernstein, 1865 |
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| Tagula Manucode | *Manucodia alter* | (Lesson, 1830) |
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| Ribbon-tailed Astrapia | *Astrapia mayeri* | Stonor, 1939 |
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| Eastern Parotia | *Parotia helenae* | De Vis, 1897 |
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| King of Saxony Bird of Paradise | *Pteridophora alberti* | A. B. Meyer, 1894 |

| | | |
|---|---|---|
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| | *L. s. feminina* | Ogilvie-Grant, 1915 |
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| | *L. (s.) niedda* | Mayr, 1930 |
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| | *P. m. jobiensis* | Rothschild, 1897 |
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| | | |
|---|---|---|
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| Emperor Bird of Paradise | *Paradisaea guilielmi* | Cabanis, 1888 |
| | Genus *Paradisornis* | Finsch & A. B. Meyer, 1885 |
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| | *P. r. margaritae* | Mayr & Gilliard, 1951 |

## Formerly classified as birds of paradise

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| Crested Satinbird | *Cnemophilus macgregorii macgregorii* | De Vis, 1890 |
| | *C. m. sanguineus* | Iredale, 1948 |
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| | *A. s. cinnamomeus* | Mees, 1964 |
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| Black-eared Catbird | *Ailuroedus melanotis melanotis* | (G. R. Gray, 1858) |
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| | Genus *Archboldia* | Rand, 1940 |
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| | | |
|---|---|---|
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| Flame Bowerbird | *Sericulus ardens* | (D'Albertis & Salvadori, 1879) |
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| Regent Bowerbird | *Sericulus chrysocephalus* | (Lewin, 1808) |
| | Genus *Ptilonorhynchus* | Kuhl, 1820 |
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| | Genus *Chlamydera* | Gould, 1837 |
| Western Bowerbird | *Chlamydera guttata guttata* | Gould, 1862 |
| | *C. g. carteri* | Mathews, 1920 |
| Great Bowerbird | *Chlamydera nuchalis nuchalis* | (Jardine & Selby, 1830) |
| | *C. n. orientalis* | Gould, 1879 |
| Spotted Bowerbird | *Chlamydera maculata* | (Gould, 1837) |
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Particular thanks are owed to John Cantelo, who read multiple drafts of the text, patiently fielded queries and suggested many improvements. Nigel Redman instituted the *Birds of Paradise and Bowerbirds* project and was very understanding over various unforeseen interruptions, later followed by Jim Martin and Alice Ward, who took the project on to its conclusion. My wife Sue and son Rowan Gregory patiently supported and encouraged my work and research on the project over many years, and without them I could not have completed it. Clifford and Dawn Frith are also thanked for their exemplary scholarship with birds of paradise and bowerbirds, as also are Bruce Beehler and Thane Pratt, whose New Guinea field guides have been an essential companion for many years and whose classic *Birds of New Guinea: Distribution, Taxonomy and Systematics* (2016) will be the default reference for years to come. The inspirational *Birds of Papua New Guinea* by Brian Coates was also an essential reference, with much insight into the two families.

It is unusual to have two quite distinct families in a single volume, but there is a long historical precedent for it, with many famous titles in both the 19th and the 20th centuries. In 1977, Forshaw and Cooper produced a wonderful volume entitled *The Birds of Paradise and Bowerbirds*, with the large-format illustrations conceivably the best since the days of lithography in the previous century. The two families are singularly attractive and unique groups from the same zoogeographical region, and together they exhibit some of the most elaborate and bizarre plumages and behaviours in the avian kingdom. For the present work Richard Allen was available as the artist, using his remarkable flair for depicting iridescent plumages and both accurately and attractively depicting the birds themselves. Together with the beautiful photographs sourced from many different people, I believe we have a winning combination that celebrates and details these two wonderful bird families.

Many other people helped in various ways, from field companionship and discussion on taxonomy, identification, sound recordings and general advice to travel logistics, and my thanks go to all: Stephen Ambrose, Joseph Ando, Kim & Paul Arut, Kenneth & Tanya Arut, Bob Bates, Untu Baware, Tony Baylis, Andrew Bowes, the late Ian Burrows, the late Barbara Burrows, Dominic Chaplin, Brian Coates, David Donsker, Jack Dumbacher, Brian Finch, Chris Eastwood, Andy Elliott, Mat Gilfedder, Judith Giles, Frank Gill, Will Goulding, Benson Hale, Roger Hicks, Betty & Peter Higgins, Dion Hobcroft, the late Jon Hornbuckle, Josep del Hoyo and Arnau Bonan Barfull for the marvellous resource that is *HBWAlive* and the *Internet Bird Collection* (IBC), Phil Hurrell, the late Steven Ipai, David James, Pak Jamil at Nimbokrang, Markus Lagerqvist, Tim Laman, Mary LeCroy, Murray Lord, Sharon Mackie, Max Male, Jun Matsui, David Mitchell, Lloyd Nielsen, Moyang Okira, Max Pakao, Jan Pierson, Shita Prativi, Pamela Rasmussen, Rose-Ann Rowlett, Ed Scholes, Dave Stejskal, Joseph Tano, Mike Tarburton, Kisea Tiube, Karen Turner, Philip Veerman, Leonard Vaieke, Daniel Wakra, Peggy Watson, Richard Webster, Bret Whitney, Zeth Wonggor, and Iain Woxvold; and I have appreciated working over many years with Samuel Kepuknai, Jimmy Woram, Edmund Woram and Kwiwan Sibu of what is now Kiunga Nature Tours. Sue and Rowan Gregory of Sicklebill Safaris/Cassowary Tours and the staff at Field Guides Inc. are also thanked for their great tour logistics, which enabled me to gain field experience of most of the species in this book. The late Steve Mead at the International Education Agency (IEA) in Port Moresby was a very understanding and supportive employer regarding my various New Guinea birding diversions from educational administration during 1991–97. The Victoria's Riflebirds and Spotted Catbirds at Cassowary House enlivened my authorial duties by their frequent visits while I was working on the text, and provided some useful behavioural and vocalisation insights. David Christie was enlisted as the copy editor and I have greatly benefited from his vast experience, patience and knowledge. Errors and omissions are inevitable and are the author's responsibility; please do advise of any which you come across, so that they may be corrected in any future edition.

This project began back in 1998 when my friend and colleague the late Dr Ian Burrows gave a talk to the British Ornithologists' Club in London about 'Birds of Paradise in Papua New Guinea'. Nigel Redman, from what was then Pica Press, was in the audience, and he promptly commissioned a book about the family. Ian knew that he could not do this alone, so I was invited to be a co-author and duly began putting together an overall framework for each species. Ian and our artist, Richard Allen, began work on examining specimens from the Natural History Museum at Tring (BMNH, now NHMUK), and some four years later we had a basic outline of all species prepared but awaiting plumage details. Life, families, careers and professional responsibilities then intruded, and the project was essentially placed on hold for some years. Tragedy then intervened, with Ian's untimely death in October 2009 an immense setback, which was very distressing for all concerned. Following some changes at the publishing house, Jim Martin became the editor and proved keen to get the project restarted. My own touring and publishing commitments precluded an immediate start, but things gradually resolved and I was happy to be able to conclude the long-gestating work. I dedicate it to Ian and his brilliance and just wish that he had been able to take part in it. I sincerely hope that readers find it worthy of his memory.

The information in these introductory sections is derived from a wide variety of sources, both electronic and printed, but I gratefully acknowledge the huge debt owed to the many researchers and scientists who are gradually unearthing the details of the biology of these fascinating and still quite poorly known families. Foremost among them have to be Drs Clifford and Dawn Frith, who have devoted their working lives to research on both the birds of paradise and the bowerbirds, and Dr Bruce Beehler, whose contributions to the biology of these families from New Guinea are immense. Their monographs on *The Birds of Paradise* (Frith & Beehler 1998, OUP) and *The Bowerbirds* (Frith & Frith 2004, OUP) are the fountainheads of knowledge, and we refer readers to these works for the vast amounts of detailed information and background data painstakingly acquired over many years and which are not appropriate for a more general overview such as this current title. We also acknowledge the contributions from the monumental *Handbook of the Birds of Australia and New Zealand and Antarctica* (HANZAB), the late E. T. Gilliard's classic work *Birds of Paradise and Bowerbirds* (1969), Peter Rowland's invaluable short work on *Bowerbirds,* and of course the phenomenal resource *Handbook of the Birds of the World,* now in electronic format as *HBWAlive.* Here, the work of the Friths and Arnau Bonan has been most instructive and we again acknowledge our debt to them in making this marvellous archive accessible.

No work on the birds of paradise is complete without acknowledgement of the brilliant work of Tim Laman and Ed Scholes in the *Bird of Paradise Project.* They have for many years been photographing and making videos of the paradisaeids, and their recordings of the displays of most species are a fantastic resource and archive. Their book *Birds of Paradise* (National Geographic 2012) is quite simply the most astonishing collection of photographs of these extraordinary birds ever. Thanks to funding from the Cornell Lab of Ornithology, National Geographic Expeditions Council and Conservation International, they have forayed to the most remote parts of New Guinea in quest of these species. By 2011, they had archived every single paradisaeid, the project by then having taken some eight years, with 18 expeditions to 51 different field camps. By their own account they had climbed hundreds of trees, built dozens of hides, and made thousands of video and audio recordings, with more than a year and a half spent in the field, and taken more than 39,000 photographs.

One of the great discoveries that has emerged from their studies is that female birds of paradise often watch males from very specific viewpoints. A proper understanding of the displays ideally requires the capacity to see what the female sees, and an innovative camera set-up has now allowed them to film this viewpoint for the Wahnes's Parotia. The plan now is to document this perspective for all the other species, and the project continues.

Their latest contribution (2017) was a landmark paper concerning the courtship and displays of the poorly known *Astrapia* species, with some remarkable discoveries arising from the careful study of thousands of hours of audiovisual material vouchered at the Cornell Lab of Ornithology.

*Phil Gregory*

# INTRODUCTION

## What is a bird of paradise? The family Paradisaeidae

The very name 'bird of paradise' has an exotic and rather romantic ring to it, and this is surely one of the most iconic, striking and simply extraordinary bird families in existence. The name has gone through various iterations, such as bird of paradise, Bird-of-paradise, Bird-of-Paradise and Bird of Paradise, the last a form that was in use early in the last century and which is perhaps the most pleasing to the eye, shorn of extraneous hyphens and featuring capitals for both nouns. Nevertheless, the modern style dictates that we should restrict the capitalisation to the level of species names alone, and this is, with some reluctance, followed here.

The birds of paradise are a very well-known and truly remarkable radiation of species, justly celebrated for their extraordinary diversity of courtship behaviours and bizarre exotic plumages derived from sexual selection. The 43–45 species evolved over roughly 20 million years, with most ornamental phenotypic evolution occurring within the core birds of paradise (all but the basal *Manucodia/Lycocorax* clade) over the last 15 million years, and sometimes considerably more recently, as with the *Paradisaea* group (Laman & Scholes 2012; Scholes *et al.* 2017).

The question of what makes a bird of paradise a bird of paradise is, however, frequently asked, and the answer is perhaps surprisingly not particularly easy to formulate. The family Paradisaeidae is very diverse in form and coloration and includes some of the most spectacular and striking species of bird, but what defines them? Several features are shared by all the species: they all have a chunky and quite stout body shape, but with huge variation in bill and tail size and shape. None of them can be considered a great songster, either. Most have harsh, resonant or strident calls, a few more melodious than others, but there is none that can be considered an outstanding musical vocalist. Most of them are primarily frugivorous, from environments where this resource is often abundant and allows plenty of time for other activities such as courtship and displays. Many have unusually striking displays, be it from dancing grounds, songposts or canopy display sites. Apart from the earliest evolved species, the manucodes and paradise-crows, which are monogamous, the birds of paradise are polygynous, the promiscuous males performing displays to attract females, which choose which male to mate with. Most (but not all) of the polygynous species show marked sexual dimorphism.

Birds of paradise were formerly considered closely related to bowerbirds, and sometimes even combined with that family in either Paradisaeidae (Stresemann 1934a; Gilliard 1969) or Ptilonorhynchidae (Sharpe 1891–98; Schodde 1975; Cracraft 1981), owing to certain similarities in zoogeography, chunky body shape, sexual dimorphism and polygynous breeding strategy. As the sum of knowledge grew, however, it was realised that major differences exist, though the birds-of-paradise are, anatomically, broadly typical of the oscine passerines, and are generally somewhat crow-like in many ways.

- Adult male plumage of many of the paradisaeids includes striking iridescence, with an amazing range of extremely bright plumages not otherwise found among the corvoid assemblage.
- Egg coloration is different in each family, the birds of paradise laying attractively coloured eggs, typically decorated with broad dark brush-like streaks.
- Birds of paradise have a distinctive flap-and-glide undulating flight, and the wings of adult males in many genera (especially *Astrapia* and *Ptiloris*) produce a characteristic rustling sound in flight.
- Eggs are laid on consecutive days by many birds of paradise, but on alternate days by many bowerbird species.
- Nestling plumage differs: young birds of paradise lack down and have dark skins, whereas bowerbird nestlings are very downy and pale-skinned.
- Birds of paradise feed their young by regurgitation, a method not used by bowerbirds when feeding their young.
- There are large differences in skull osteology between the two families, birds of paradise skulls technically having a small or non-existent lachrymal and, consequently, a large ectethmoid plate solidly fused with the frontal bone, and a short orbital process of the quadrate with an expanded distal tip (Frith *et al.* 2017).

- Birds of paradise are not known to cache food, whereas this behaviour is habitual in some bowerbird species.
- Birds of paradise do not use vocal mimicry, whereas many bowerbirds are accomplished mimics.
- The loud bugling or far-carrying calls of many birds of paradise have no equivalent in bowerbirds.
- Nest structure differs between the two families, with the birds of paradise constructing nests made of the long supple stems of epiphytic orchids and vines; in contrast, bowerbirds use a woody stick base when nesting.
- Many birds of paradise use arenas or courts, and none of them uses sticks or vegetation for construction purposes; the use by the males of stick bowers for display is restricted to bowerbirds.
- Elements of the displays differ greatly, and the hide-and-peek display of many bowerbirds is unknown among the paradisaeids.
- Tool use is a very rare habit among birds and unknown among paradisaeids, while several species of bowerbird are known regularly to use a form of tool to paint their bowers.
- Bill size and shape have a very diverse range in the paradisaeids, but are relatively uniform among the bowerbirds.
- Both birds of paradise and bowerbirds have 12 rectrices and ten primaries, but bowerbirds have an atypically large number of secondaries (11, or 14 including the tertials). Paradisaeids have eight secondaries (11 if one includes the tertials).
- Hybridisation, rare to uncommon in birds generally, is quite widespread among birds of paradise, with a variety of hybrids known (including some intergeneric pairings), but it is very rare among bowerbirds.
- Birds of paradise habitually use their large and strong feet to hold and manipulate food items, something not done by bowerbirds.

Stonor (1937) found no evidence that the two families were closely related, and classified the birds of paradise as a distinct family with no close relatives. Sibley & Ahlquist (1985, 1990) and their pioneering studies of DNA–DNA hybridisation also found no close relatives, but showed that the bowerbirds were in fact part of the great corvoid songbird lineage. Christidis & Schodde (1991) showed a relationship with Artamidae (butcherbirds, woodswallows etc.), and later studies also reveal them as a monophyletic family (Kusmierski *et al.* 1993).

Ornithologists formerly treated the bird of paradise family, Paradisaeidae, as being closest to the bowerbirds (Ptilonorhynchidae), even after avian anatomists published contrary views. Indeed, some combined the bowerbirds and the birds of paradise into a single family, the Paradisaeidae. Research reveals that the majority of Australasian passerines, about 85% of the total, derives from a southern, or Gondwanan, origin. This major group, referred to as the 'Corvida', radiated in Australia and New Guinea, and today comprises three major lineages or superfamilies:

- Menuroidea, which includes the lyrebirds and Australasian treecreepers (Climacteridae), as well as bowerbirds.
- The Meliphagoidea, which includes honeyeaters and their allies.
- The Corvoidea, which includes the birds of paradise (Frith *et al.* 2017).

Genetic research revealed the major distinctions between the paradisaeids and the bowerbirds, in tandem with increasing biological evidence that also showed a major dichotomy between the two families. Birds of paradise were found to be not only distinct from the bowerbirds but also relatively distant from them in evolutionary terms. Current genetic research indicates that the separation of the birds of paradise from the bowerbirds occurred some 28 million years ago, this finding being based on molecular-clock calibrations, which are still being refined and resolved.

The ground-breaking genetic research of Sibley & Ahlquist (1990), based on what was then a new technique of avian DNA–DNA hybridisation, showed the Paradisaeidae as the sister-group to the radiation now comprising the woodswallows and butcherbirds (Artamidae), the Old World orioles (Oriolidae) and the cuckooshrikes (Campephagidae). Going back one level, the crows and their allies (Corvidae) form the sister-group to this lineage. Later passerine phylogeny, based on two single-copy nuclear-gene sequences, places Paradisaeidae close to the apex of what is termed the 'core Corvoidea', along with Australian mudnesters (Struthideidae), monarchine flycatchers (Monarchidae) and true corvids.

Besides bowerbirds, a number of species or groups, including the silktails (*Lamprolia*) of Fiji, the Kokako (*Callaeas*) and saddlebacks (*Philesturnus*) of New Zealand (wattlebirds) and the Lesser Melampitta (*Melampitta lugubris*) of highland New Guinea, have been suggested as members of the Paradisaeidae family. More recent work has placed the New Zealand wattlebirds as their own ancient family, Callaeidae, while the melampittas, too, are now allocated an ancient family of their own, Melampittidae, and the silktails look likely to be placed in their own family of Lamproliidae, along with the Pygmy Drongo-fantail (*Chaetorhynchus*) of New Guinea.

There have been major adjustments within the family in the past two decades, and four species that were formerly classified as birds of paradise have been reallocated, following genetic studies revealing their true placement.

For decades the Crested (*Cnemophilus macgregorii*), Loria's (*C. loriae*) and Yellow-breasted Birds of Paradise (*Loboparadisea sericea*) comprised the 'wide-gaped' paradisaeid species of the subfamily Cnemophilinae. These three, which we now call satinbirds, were always an uneasy and atypical fit among the true Paradisaeinae, as they possess a very different skull morphology and a rather small, delicate bill and feet. Their behaviours are also completely different, the satinbirds not using their feet to hold prey items, and having the wide gape indicative of an almost entirely frugivorous diet. Their vocalisations also are very different; they build domed nests with a side entrance; and they do not hold court or have obvious displays. In addition, they have a distinct juvenile plumage, which is lacking among the birds of paradise.

For many years the classification of the satinbirds was uncertain, some authorities interpreting the cnemophiline cranial and mandibular osteology as indicative of a basal sister-group to the main paradisaeine lineage. The uncertainty was resolved through genetic studies, which showed that the cnemophilines form a quite distinctive group, part of a clade which also contains the New Guinea berrypeckers and longbills (Melanocharitidae) and the New Zealand wattlebirds (Callaeidae). They are thus quite distant from the true birds of paradise, being rather a basal part of the oscine assemblage and indeed more closely related to bowerbirds, with which they share some skull characters. The three cnemophilines now comprise the satinbird family, endemic to New Guinea and named for the rather glossy textured plumage of the males.

The other species reclassified from the Paradisaeidae is a large and striking one formerly called 'MacGregor's Bird of Paradise' (*Macgregoria pulchra*), a highly prized species difficult for birders to find, and previously another anomaly in the family. This spectacular high-altitude and restricted-range montane endemic was shown by genetic work (Cracraft & Feinstein 2000) to belong to the family of honeyeaters (Meliphagidae), and not to the birds of paradise. As with many honeyeaters, it is largely frugivorous. During fieldwork in 1991, its active behaviour had been noted as resembling that of honeyeaters and the yellow facial wattle was seen to blush orangey (Gregory & Johnstone 1993), reminiscent of Smoky Honeyeaters (*Melipotes fumigatus*). It was formerly treated as one of the basal members of the Paradisaeinae, and was very little known. The common name has proven vexatious in recent times, and both 'Ochre-winged Honeyeater' and 'Giant Wattled Honeyeater' have been used, neither being particularly appropriate and the latter inviting confusion with the giant honeyeaters of Fiji. Here we maintain the historic vernacular name, which commemorates Sir William MacGregor, the first governor of the Territory of Papua and New Guinea, and treat the species in an appendix along with the satinbirds. All four of these former birds of paradise are covered briefly in the addendum, and also illustrated for the sake of completeness and as a recognition of the historic links between the species.

The family Paradisaeidae as treated here comprises 45 species (following the split of the former 'Superb Bird of Paradise'), in 16 genera, with a current total, including subspecies, of 71 taxa. Most occur in New Guinea and its satellite islands, which have 40 species, two of these, the Trumpet Manucode (*Phonygammus keraudrenii*) and Magnificent Riflebird (*Ptiloris magnificus*), extending also to Cape York, in extreme north-east Queensland, Australia. Two of the four *Ptiloris* riflebirds are found only in east Australia, where they are endemic in eastern Queensland and New South Wales. Away from New Guinea and Australia, there are three other members of the family in the North Moluccas of Indonesia, one in the monotypic genus *Semioptera* (Wallace's Standardwing *S. wallacii*) and the two species of paradise-crow (*Lycocorax*).

The six species of manucode and the two paradise-crow species have a monogamous breeding strategy. This is in contrast to the other 33 polygynous species in the family, the promiscuous males of which attract females to traditional solitary courts, display perches or communal leks, where they court and mate with them.

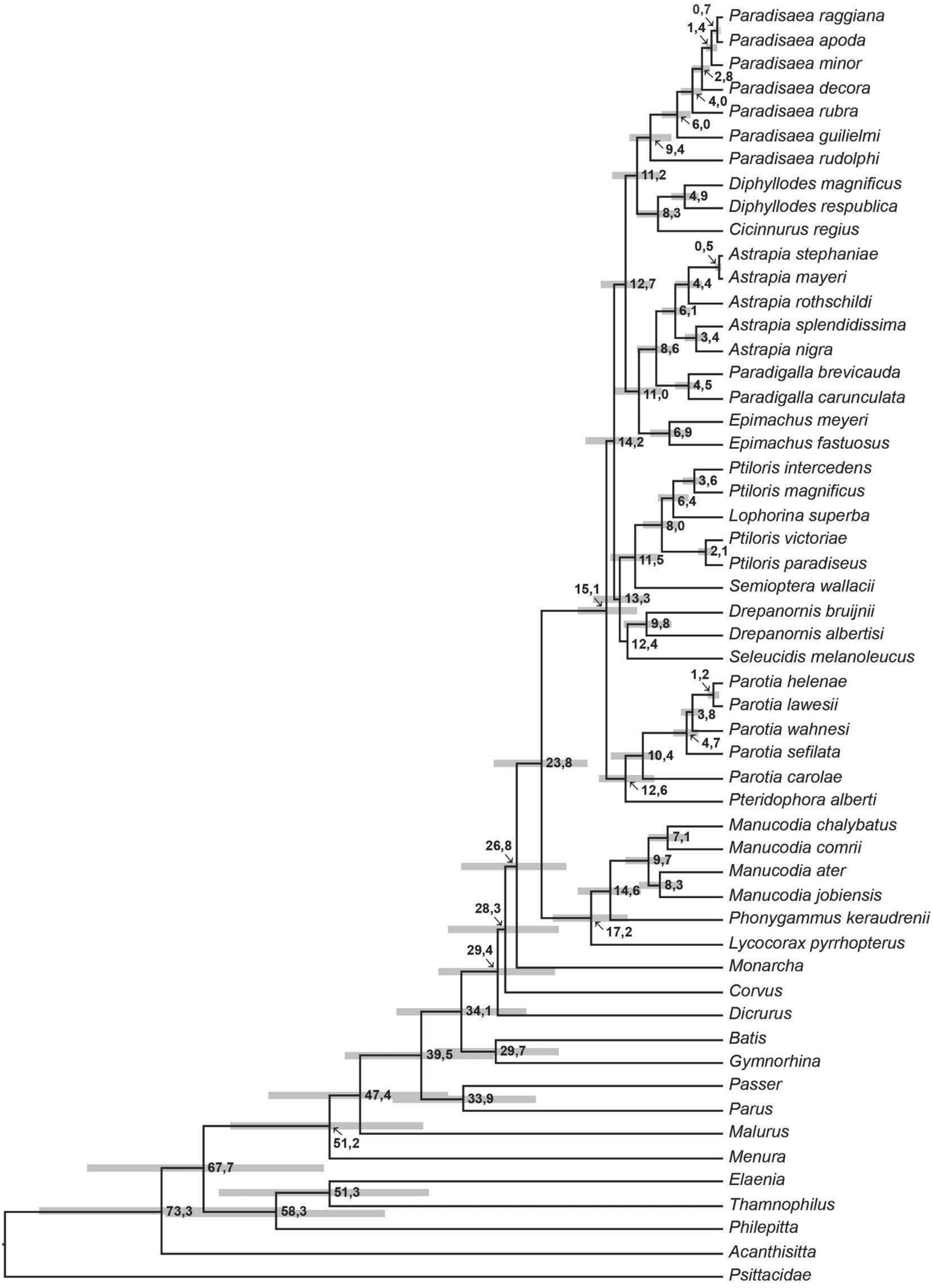

**Figure 1. Chronogram with divergence-time estimates of the birds of paradise**. The divergence times and confidence intervals (grey bars) were estimated under a relaxed clock model implemented in Beast 1.4.7. For the calibration of the chronogram the postulated separation of *Acanthisitta* from all other passerines in the phylogeny was used. (Reproduced by kind permission from Irestedt *et al.* 2009)

From the mid-20th century there was a long-standing stability in respect of what constituted the bird of paradise family, and the number of constituent species stayed much the same. Over the past 25 years or so, however, there have been gradual changes and some drastic re-evaluations of what species are involved, and how they are defined. The well-established and generally accepted biological species concept (BSC), defined by whether or not different species can interbreed and raise fertile young, held sway for much of the latter part of the last century. Some difficulties arise, though, when attempting to apply this concept to allopatric groups where similar-looking taxa do not actually come into contact, so the interbreeding hypothesis remains hypothetical. Modifications have been proposed and broader, more flexible definitions are now often utilised. When the phylogenetic species concept (PSC) was applied to the group, based on often minor physical features weighing very heavily as taxonomic signifiers, the result was a dramatic increase in the number of constituent paradisaeid species recognised, to about 90 (Cracraft 1992). This taxonomic treatment has not received wide recognition, but it does shed light on relationships within the family, and further refinement and taxonomic research continue apace.

## Origins and species diversification

The family Paradisaeidae comprises two well-defined lineages, one being the manucodes and the paradise-crows (*Lycocorax*) and the other being the 25 species of plumed paradisaeid. *Paradigalla* seems also to be a basal form, while *Astrapia* may be a sister-group to the plumed birds. Manucodes and paradise-crows are distinctive, with dark plumage, special syrinx morphology and monogamous nesting habits, and can be regarded as constituting at least a valid subfamily. A study by Irestedt *et al.* (2009) revealed five main clades in their phylogeny.

- **The first clade (A)** consists of manucodes (*Manucodia* and *Phonygammus*) and the paradise-crows (*Lycocorax pyrrhopterus*). This clade is supported as the sister-group to the core birds of paradise (remaining genera).

A very significant finding here was that the split between the *Manucodia–Lycocorax* clade and the core birds of paradise clade was estimated to have occurred about 24 million years ago, while the basal divergence of the polygynous core birds of paradise was suggested to be around 15 million years old. 'The age estimates further suggest that generic separations occurred between six and 14 million years ago, while speciation within genera mostly occurred between 0.5 and ten million years ago.' The origin seems, therefore, to date back to late Oligocene and early Miocene periods, with much speciation later in the latter epoch.

Other studies have indicated that the manucodes and the plumed paradisaeine lineages may have diverged from each other from about 20–18 million years ago to as recently as about seven million years ago. Calibrating the genetic clock remains a work in progress, but much has been learned of the evolutionary history thanks to these important studies.

## The plumed paradisaeids

Genetic studies (Irestedt *et al.* 2009) indicate that all the plumed paradisaeid species seem to derive from a single radiation. These plumed taxa can be divided into four morphologically well-defined clades, with manucodes and *Lycocorax* as the first clade, although genetic work gives a slightly different arrangement (see below).

- **The second clade (B)** consists of the King of Saxony Bird of Paradise (*Pteridophora alberti*) and the parotias (*Parotia*). Within this clade Carola's Parotia (*Parotia carolae*) is highly divergent and warrants separate generic treatment. These are sometimes referred to as the 'flagbirds', the males with spectacular erectile occipital plumes, velvety-black dorsal plumage, an iridescent throat or breast patch, and highly distinctive courtship displays.

- **The third clade (C)** consists of the Twelve-wired Bird of Paradise (*Seleucidis melanoleucus*), the *Drepanornis* sicklebills, Wallace's Standardwing, the riflebirds (*Ptiloris*) and the lophorinas (*Lophorina*). Support for more basal nodes within this clade, however, is low, and the affinity of the Twelve-wired Bird of Paradise, *Drepanornis* sicklebills and the Wallace's Standardwing should be regarded as provisional. Although bootstrap values are low, New Guinean *Ptiloris* and *Lophorina* together form a clade separate from the Australian *Ptiloris*. This apparent relationship suggests a significant phylogenetic break between Australia and New Guinea, although a study by Irestedt *et al.* (2017) found no support for this seeming divergence. Riflebirds and lophorinas all have a striking large iridescent blue breast shield, displays based around

**King of Saxony Bird of Paradise**, adult male, PNG (*Shutterstock*).

song-posts atop vertical snags or logs, and harsh but relatively simple display songs. They appear to have diverged about four million years ago and are sister to the parotias and King of Saxony group, with more distant links to sicklebills and the plumed paradisaeids. Note that the recent HBW–BirdLife taxonomy (del Hoyo & Collar *et al.* 2016) merges *Ptiloris* into *Lophorina*.

The sicklebills (*Epimachus* and *Drepanornis*) constitute two closely related but distinct lineages, the two very long-tailed *Epimachus* ('sabretails') having marked sexual dimorphism, iridescent crown and mantle feathering, red or pale blue iris, and the chin and throat lacking barring in both sexes. The Irestedt *et al.* (2009) phylogeny placed *Epimachus* as sister to a clade that includes *Paradigalla* and *Astrapia*, implying that the long, curved bill has been independently acquired in relation to *Epimachus*.

Characteristic of the *Drepanornis* Black-billed (*Drepanornis albertisi*) and Pale-billed (*D. bruijnii*) Sicklebill species pair are a much shorter tail, much less marked sexual dimorphism and bare facial skin, and both sexes have a brown iris and barred chin and throat. Irestedt *et al.* (2009) positioned *Drepanornis* as sister to a clade that includes *Ptiloris*, *Lophorina* and *Semioptera*.

- **The fourth clade (D)** includes the long-tailed *Epimachus* sicklebills, paradigallas (*Paradigalla*) and astrapias (*Astrapia*).

The two rather poorly known *Paradigalla* species constitute a lineage of obscure affinities. The black plumage and egg morphology link them to basal taxa such as *Manucodia*, but there are also resemblances to *Astrapia* regarding habit, plumage, and body and bill morphology. *Paradigalla* was shown to be sister to *Astrapia* by Irestedt *et al.* (2009), and subsumed within *Astrapia* by Dickinson & Christidis (2014), but, given the substantial morphological, behavioural and vocal distinctions, we feel it best to retain *Paradigalla*.

*Astrapia* seems to be allied also to the plumed lineage in terms of the male's ornate erectile head and mantle feathering, the barred underparts of females, and the egg morphology. Conversely, the mainly black plumage of the two sexes may link *Astrapia* to the basal paradisaeid taxa, although the black plumage, iridescent head and breast feathering and simple harsh vocalisations may equally suggest a link to *Ptiloris* riflebirds.

- **The fifth clade (E)** consists of the *Paradisaea* birds of paradise and the three sickletails – Wilson's Bird of Paradise (*Cicinnurus respublica*) and Magnificent Bird of Paradise (*C. magnificus*), both formerly placed in

*Diphyllodes*, and the King Bird of Paradise (*C. regius*). Within this clade the genera *Diphyllodes* and *Cicinnurus* were sister lineages (with *Diphyllodes* now subsumed into *Cicinnurus* in subsequent treatments), while the Blue Bird of Paradise (*Paradisornis rudolphi*) is sister to other *Paradisaea* species (and was formerly placed in *Paradisaea*).

These plumed species form a complex clade with several sublineages. It comprises the four genera *Cicinnurus*, *Semioptera*, *Seleucidis* and *Paradisaea*, linked by several shared characters. Adult males have iridescent green and brilliant red and/or yellow areas in the plumage, emit loud harsh, scolding *Paradisaea*-type advertisement vocalisations, and have display postures. The three diminutive *Cicinnurus* species (sickletails) have the central pair of rectrices modified into recurved 'wires', with iridescent green plumage on the underparts, red dorsal plumes, and bright blue legs and feet. We follow recent authorities in merging *Diphyllodes* into *Cicinnurus*; see Dickinson & Christidis (2014), Gill & Donsker (2017) and Beehler & Pratt (2016).

The *Paradisaea* genus is defined by the presence in adult males of both filamentous elongated flank plumes and grossly elongated wire-like or tape-like central rectrices. This sublineage contains the seven 'true' plumed bird of paradise species, namely the Lesser Bird of Paradise (*Paradisaea minor*), Greater Bird of Paradise (*P. apoda*), Raggiana Bird of Paradise (*P. raggiana*), Goldie's Bird of Paradise (*P. decora*), plus three more aberrant plumed species, namely the Red Bird of Paradise (*P. rubra*), Emperor Bird of Paradise (*P. guilielmi*) and the rather divergent Blue Bird of Paradise which is now placed in a monospecific genus.

The monotypic genera *Semioptera* and *Seleucidis* are the final members of the clade. Wallace's Standardwing is an aberrant member of the family restricted to the Moluccas, and appears to be a sister form of the *Cicinnurus*–*Paradisaea* group, supporting evidence being the green adult male breast plumage and the zoogeographical proximity to those genera. The Twelve-wired Bird of Paradise is also quite aberrant, showing characters associated with two other sublineages: the black adult male plumage, heavily barred female, long decurved bill and tree-stump display sites link it to the riflebirds, while the filamentous yellow flank plumes, *Paradisaea*-type advertisement vocalisations and displays, plus pale leg and iris colours suggest links to the *Paradisaea* lineage, but quite how to rank the evolutionary significance of these characters remains problematic.

Irestedt *et al.* (2009) propose that the main reason why the core birds of paradise, unlike other corvoid bird families, have diversified only within New Guinea and islands in the immediate vicinity is linked with their promiscuous breeding system in which just a few males acquire most of the mating opportunities. A similar sedentary life strategy, with limited dispersal outside mainland areas (and islands which have been connected with these areas) is evident in several other families with elaborate male plumages, such as the pheasants (Phasianidae), and several New World families such as manakins (Pipridae) and the polygynous species within the cotingas (Cotingidae).

Unlike the situation with bowerbirds, where hybridisation is very rare, this phenomenon is very well documented among the birds of paradise, most of the resultant forms being given vernacular names and some having historically been recognised as species. These hybrids are listed under the various species accounts. At least seven different intrageneric hybrid combinations are known, and, unusually, 13 different variations of intergeneric crosses have been recorded. This reflects the close genetic relationships within the family despite the often extreme morphological distinctions among the species. The only other family with such variety would be among the wildfowl, again where many species are closely related. It is only among the polygynous paradisaeid species that hybridisation in the wild is known, but this is not too surprising given the proclivities of the promiscuous males to mount any female-plumaged birds that come close to their display areas. Young or inexperienced birds may presumably mate with the wrong species in error, or where at the extremity of habitat or range there may be no other mate available.

## Patterns of speciation and diversification

It is suggested that the reproductive strategies used by birds of paradise may have constrained their capacity to disperse, as they are so dependent upon habitats that have a great diversity of fruiting tree species. In addition, it is likely that the complex ornamental plumes and intensive displays are a limiting factor, as is the strong attachment to display sites. Furthermore, males and females generally live separately, except during the mating period, which makes it less likely that successful long-distance dispersal and establishment of new breeding populations can occur.

The genera *Manucodia*, *Phonygammus*, *Paradigalla* and *Lycocorax* are monomorphic, with the sexes very similar to each other in appearance, and they are monogamous, forming pair bonds, quite unlike the promiscuous behaviour of the rest of the family. This simpler and less complex life strategy perhaps enabled these birds to have a higher dispersal capacity, which could explain the present-day occurrence of *Manucodia* and *Phonygammus* on several islands off the New Guinea coast and on Australia's Cape York Peninsula, and of *Lycocorax* on the North Moluccas. Conversely, *Paradigalla* is a genus restricted to the main New Guinean mountain ranges and does not occur in the coastal lowlands, which renders it less likely to disperse. The present-day distribution of Wallace's Standardwing in the North Moluccas is more difficult to explain. A late-Miocene origin seems probable for this species, at a time when the Moluccas were located much closer to what is now the Vogelkop Peninsula. These monomorphic groups are believed to be among the most ancient in the family, so the timespans involved may have permitted more dispersal.

The paradisaeid genera *Astrapia*, *Ptiloris* and *Paradigalla* have distinct allopatric clades in both the east and the west of New Guinea, which separated about 3–6 million years ago. This **allopatric speciation** model appears also to be the major source of diversification in *Paradisaea*, the mainland lowland species complex of which originated quite recently in the Pleistocene, while the island endemic Red and Goldie's Birds of Paradise appear slightly older. In this genus all lekking species are morphologically very homogeneous, although the age of the genus is more than six million years (the split between Emperor Bird of Paradise and other lekking *Paradisaea* species). The Emperor Bird of Paradise and the highly divergent montane Blue Bird of Paradise are much older divergences. Similarly, the morphological variation is modest within the genus *Parotia*, for which the exploded lekking system is estimated to be around ten million years old. The divergences within the New Guinea and Australian riflebirds (*Ptiloris*) correspond to broad land connections in the upper Miocene and marine transgression in the Pliocene when the land bridges were flooded.

Heads (2001b, 2002) postulated that the present-day distributions of birds of paradise in New Guinea are difficult to explain simply by Pleistocene refugia processes, and relate rather to historic terrane movements over a longer timespan. He used three bird of paradise genera (*Astrapia*, *Parotia* and *Paradisaea*) in support of his thesis, assuming sister relationships with a strong biogeographical connection between the species occurring in the Vogelkop, West Papua, and those in the Huon Peninsula, Papua New Guinea. The phylogeny of Irestedt *et al.* (2009), however, does not provide support for this biogeographical scenario. A sister relationship between the Western Parotia (*Parotia sefilata*) in the Vogelkop and Wahnes's Parotia (*P. wahnesi*) from the Huon Peninsula is only weakly supported, while within the genus *Astrapia* their phylogeny conversely strongly indicates sister relationships between species that occur in closely connected geographical areas (between the Huon Peninsula

**Western Parotia**, adult male in display, West Papua, Indonesia (*Marek Stefunko*).

and the Central Highlands, and between the Vogelkop and the Star Mts). Oddly, though, some elements of the display of the Huon Astrapia (*Astrapia rothschildi*) do bear some resemblance to what is known of the Arfak Astrapia (*A. nigra*). Within the genus *Paradisaea*, the Emperor Bird of Paradise from the Huon Peninsula is sister to all other *Paradisaea* species that occur in most of lowland New Guinea (excluding the morphologically rather divergent montane Blue Bird of Paradise, which is now allocated to a different genus).

The sicklebills present what may well be an instance of quite ancient altitudinal speciation, with the two *Drepanornis* species separating ten million years ago and the two *Epimachus* species about seven million years ago. Black-billed and Pale-billed Sicklebills (*Drepanornis*) occupy different elevations in lowland and mid-montane forests, while the Black (*Epimachus fastosus*) and Brown Sicklebills (*E. meyeri*) replace each other altitudinally in mountain forests. Likewise, the montane and patchily distributed Lawes's Parotia (*Parotia lawesii*) and Eastern Parotia (*P. helenae*) may represent a more recent altitudinal speciation event, similar instances of which are exhibited by various other bird families, e.g. the honeyeaters (Meliphagidae) and the scrubwrens and gerygones (Acanthizidae).

Irestedt *et al.* (2009) conclude that divergence-time estimates for birds of paradise indicate an older clade than previously suspected. Diversification within several genera of birds of paradise seems to have been a continuous process through the Tertiary period, the younger divergences (as in *Paradisaea*) being geographically quite closely linked. Besides allopatric speciation, there appear to be examples also of altitudinal speciation.

The observation that sexually dimorphic polygynous genera are morphologically homogeneous is particularly interesting, despite divergences between species being suggested as being several million years old. These calculations of diversification rates indicate that the speciation rate is in fact not excessively high. It can be argued that sexual selection in birds of paradise appears not to have generated a particularly rapid change in sexual ornamentations or a markedly high speciation rate. This tentative explanation remains uncertain, although the long generation time of polygynous male birds of paradise coupled with extensive hybridisation may have constrained morphological diversification and speciation. Ecological factors such as abundant food sources may also explain why male birds of paradise have been able to develop and maintain their promiscuous breeding systems, magnificent plumages and elaborate courtship displays.

Birds of paradise have undergone some recent taxonomic changes, with the Growling Riflebird (*Ptiloris intercedens*) a long overdue split and the Obi Paradise-crow (*Lycocorax obiensis*) another, while the three-way split of the Superb Lophorina (*Lophorina latipennis*) has now been proposed and is tentatively accepted in the present work. In the manucode subfamily, the Tagula Manucode (*Manucodia alter*) is recognised here as

**Brown Sicklebill**, female feeding, Kumul Lodge, PNG (*Shane P. White*).

distinct, and it is clear that the Trumpet Manucode consists of at least four cryptic species, which await further clarification regarding their vocalisations. We indicate where further splits are likely. Generic realignments also have occurred, with *Diphyllodes* merged into *Cicinnurus* and the Blue Bird of Paradise moved into *Paradisornis*, although we have resisted the trend to merge *Ptiloris* with *Lophorina* and we maintain *Paradigalla* as distinct from *Astrapia* and the Trumpet Manucode *Phonygammus* as distinct from *Manucodia*.

## Plumage aberrations

Albinism as such is unknown among the birds of paradise, while leucism – formerly often termed partial albinism, which is a genetic impossibility (van Grouw 2012) – is extremely rare and known from just ten paradisaeid species. C. B. Frith (Frith & Frith 1998) examined more than 6,000 museum specimens in preparation for the family monograph (F&B 1998), finding plumage abnormalities in less than 1% of the total sample (which at that time included cnemophiline satinbirds and MacGregor's Honeyeater). The most common type of aberration was white feathering, ranging from usually a few to (rarely) more extensive white areas. The sample size may be slightly skewed by collectors obtaining the more aberrant forms, but it is clear that plumage aberrations are very rare in the family.

The following species showed minor abnormalities with varying small amounts of white feathering: Paradise Crow, Curl-crested Manucode (*Manucodia comrii*), Princess Stephanie's Astrapia (*Astrapia stephaniae*), Pale-billed Sicklebill, Blue Bird of Paradise.

More extreme examples were:

- an extensively white Splendid Astrapia (*Astrapia splendidissima*), detailed under the species account;
- a leucistic Magnificent Riflebird *sensu lato* (of unspecified taxon) with coloration entirely a pale smoky brownish-grey, with just a trace of iridescent purple-blue on the lores;
- a Magnificent Bird of Paradise that was largely white except on the breast and underparts, which were of the normal iridescent green with a few brownish back and wing feathers, with another individual that was almost entirely white;
- a Wilson's Bird of Paradise with all the underparts and most of the upperparts a deep rich fawn, with silvery-buff head and throat feathers and brownish head skin, although the yellow cape and red centre of back are present. This fits the character of non-eumelanic schizochroism, where the black pigment eumelanin is reduced, resulting in a washed-out appearance (per Harrison 1995).

**Wilson's Bird of Paradise**, adult male displaying, Waigeo, West Papua, Indonesia (*Huang Kuo-wei*).

## Habitat

Birds of paradise primarily inhabit tropical rainforests from Wallace's Line eastwards through New Guinea and extending to the east-coastal wet tropics and temperate rainforest zone of Australia. The four Australian species occur in rainforest habitats, the Paradise Riflebird (*Ptiloris paradiseus*) extending also into adjacent wet sclerophyll forest and in addition utilising nearby dry sclerophyll forest, and the Magnificent Riflebird of Cape York occupying relict rainforest and vine-forest patches. The Glossy-mantled Manucode (*Manucodia ater*) inhabits open savanna woodland, as well as rainforest, over large areas of New Guinea, while the Curl-crested Manucode lives in similar formations on the south-east islands of Papua New Guinea.

Manucodes in New Guinea have a broader habitat tolerance than other birds of paradise, some lowland forests supporting three manucode species. Each one presumably occupies a specialist niche or has specific dietary preferences, but it is not known how they co-exist ecologically. 'Habitat dictates distribution' is the rule, with most paradisaeid species in the 1,000–2,000-m zone. The Trumpet and Curl-crested Manucodes occupy wider altitudinal ranges than do any other family members, but the Trumpet Manucode appears to be an assemblage of cryptic species with at least one a montane representative. The distribution patterns of the Crinkle-collared (*Manucodia chalybatus*) and Jobi Manucodes (*M. jobiensis*) show the importance of altitude, the former being adapted to upland forest and the latter to lowland forest, though with a wide and poorly understood geographical overlap, perhaps with little or no sharing of specific habitat. Indeed, most species are habitat specialists, this being true especially of the montane ones. In Western Province of Papua New Guinea, the Crinkle-collared is the species of lowland and hill forest, with Glossy-mantled Manucode in the lowlands and Trumpet Manucode both there and in the lower hill forest to 500m.

Habitat choice seems to be quite limited among the paradisaeids, and only a few species utilise more than three habitats, the Raggiana Bird of Paradise being fairly catholic in its choice and occurring in both savanna and rainforest up to about 1,600m. The species with the most restricted ranges are those found in the mid-montane forests at 1,200–2,500m, such as the Long-tailed Paradigalla (*Paradigalla carunculata*), Huon Astrapia and various parotias. It is in this zone that the largest numbers of species occur sympatrically. Good examples of this are found in Papua New Guinea, where at the Tari Gap area at 2,100–2,500m some five paradisaeid species overlap, and at around 1,480m on Mount Missim, north of Wau, a remarkable nine species co-exist.

Congeneric species pairs are another phenomenon among various groups, including paradisaeids in New Guinea, whereby one species largely replaces another at different altitudes with only marginal overlap. Magnificent and King Birds of Paradise are a good example, the former living in upper hill and lower montane zones and the King Bird of Paradise in the lowlands and hills. Black and Brown Sicklebills demonstrate a similar example of limited overlap in mid-montane forest, the former at lower elevations and the latter at higher ones. Two Papua New Guinean endemic astrapias have partially discrete altitudinal ranges, the Ribbon-tailed (*Astrapia mayeri*) at higher altitude and Princess Stephanie's at lower levels, but they come into contact and hybridise fairly frequently where the ranges abut. Raggiana and Blue Birds of Paradise are a similar instance among closely related plumed birds of paradise, the Raggiana occurring mainly below the Blue but with overlap in some areas. The Raggiana experiences a similar situation in the upper hill forests of the Huon Peninsula of north-east New Guinea, where the Emperor Bird of Paradise inhabits the uplands and the Raggiana the lowlands.

Relatively few of the Paradisaeidae have demonstrated an ability to colonise islands across deep-water barriers, with their absence from the Bismarck Archipelago a notable example. Only ancestral forms of *Manucodia* and *Lycocorax*, plus *Cicinnurus*, *Semioptera*, *Seleucidis* and *Paradisaea* from the plumed birds of paradise, occur on islands in such areas. There are quite a few examples of seemingly anomalous distributions not readily explicable by the usual theories of biogeographical dispersion. Much remains to be learned about the influence of past tectonic events and geological processes on the present distributions of New Guinea taxa.

## General habits

The behaviour of the Paradisaeidae as a whole is not well known, and many of the more restricted-range species are almost unknown, although some other paradisaeid species have been quite well studied by scientists. Where species occur in sympatry, the mechanisms that segregate them and enable co-existence are poorly understood. A handful of species, one such being the Raggiana Bird of Paradise, have been quite well studied when breeding, but vast gaps in our knowledge remain and many research and doctoral-

**Raggiana Bird of Paradise**, male displaying to female, Varirata National Park, PNG (*Shutterstock*).

thesis opportunities beckon for those able to gain funding. Most species tend to be seen singly, although monogamous species are sometimes in pairs and there are at times aggregations at fruit sources. Up to five Victoria's Riflebirds (*Ptiloris victoriae*) have been seen loosely associating at feeders at Kuranda, in Queensland, and similar numbers have been reported in orchards. A fruiting tree at Ambua Lodge, in Papua New Guinea, is noteworthy as, when it is in peak fruit, up to five species have been seen there at the same time; Blue Bird of Paradise, Lawes's Parotia, Black Sicklebill, Brown Sicklebill and Superb Lophorina occurred simultaneously in July 2016, with up to five individual parotias at once.

From what little is known, it would appear that most birds of paradise are sedentary within small, permanent home ranges. They tend to be rather shy, flying readily and often difficult to observe. Their vocalisations are a good means of locating them, the males when breeding often calling from regular sites, particularly but not exclusively in the early morning and late afternoon. All members of the family are markedly arboreal, keeping mostly to the middle and upper levels of the forest. They will also descend to lower levels, particularly when foraging in mixed flocks. New Guinea species are very seldom seen on the ground when foraging, although the Ribbon-tailed Astrapia will descend close to it to get at the red fruits of some ginger plants. Two Australian species, the Paradise and Victoria's Riflebirds, are reported as foraging occasionally on the ground, one of the latter coming to within a few centimetres of it when piercing the nectary of some flowers at Kuranda.

A well-known phenomenon in New Guinea is the occurrence of mixed feeding or foraging flocks, often known as 'brown-and-black bird flocks' owing to the predominance of species of those colours (Diamond 1987). There is presumably some advantage to these colour combinations, perhaps involving social cohesion, lessening the chances of predation and probably disturbing more insects. The core species are often the Papuan Spangled Drongo (*Dicrurus carbonarius*), Papuan Babbler (*Garritornis isidorei*), Little Shrike-thrush (*Colluricincla megarhyncha*), Rusty Shrike-thrush (*Pseudorectes ferrugineus*), and both the Hooded Pitohui (*Pitohui dichrous*) and the Northern Variable (*P. kirhocephalus*) and Southern Variable Pitohuis (*P. uropygialis*). Pitohuis are now known to be slightly toxic and distasteful to the human palate, and there may thus be some advantage to other birds in associating with them. In the lowlands and hills such flocks will often have also Raggiana, Magnificent or King Birds of Paradise or Growling or Magnificent Riflebirds present. Other species recorded include manucodes, Princess Stephanie's Astrapia, Western, Carola's (*P. carolae*) and Lawes's Parotias, Superb

Lophorina, all the sicklebills, Twelve-wired Bird of Paradise, and other *Paradisaea* species. Flocking behaviour occurs much more among lowland-forest species than with those in upland forest, the much scarcer food resources in the latter habitat reducing flock frequency and species composition.

One interesting theory that arose from the phenomenon of brown-and-black flocks postulates that the toxic nature of some pitohuis has led to Batesian mimicry of their plumage pattern by *Paradisaea* species. The female and young of these are not typical of most paradisaeids as they lack the prominent barring shown by other birds of paradise in such plumage, but they do have rufous-brownish upperparts and a dark head, analogous with the pattern of pitohuis. Quite how this could ever be proven is uncertain, but it makes for fascinating speculation, and the apparent mimicry by various species of others here is a potentially very rewarding field of study: e.g. friarbirds (*Philemon*) with orioles, Streak-headed Honeyeater (*Pycnopygius stictocephalus*) with New Guinea Friarbird (*Philemon novaeguineae*), and immature Long-billed Cuckoo (*Rhamphomantis megarhynchus*) with Tawny-breasted Honeyeater (*Xanthotis flaviventer*).

Paradisaeids are somewhat variable in their degree of intraspecific aggression, but overall do not seem unduly pugnacious. The fruiting tree at Ambua can, as mentioned above, host five species of bird of paradise at the same time, all co-existing quite peaceably on the whole. Victoria's Riflebirds at Kuranda practise a time-share at the various feeders, almost taking it in turns to forage, albeit with males tending to dominate and fights and chases erupting occasionally, though never for very long. They are also noted as co-existing quite happily together outside the breeding season, with up to five males seen in the same area without strife. Interestingly, Spotted Catbirds (*Ailuroedus maculosus*) do dominate them at feeders.

**Predation** on birds of paradise by raptors and other non-human predators is remarkably little documented, a surprising fact given the bright plumage and loud noise of adult male paradisaeids when displaying. In some 25 years of visiting rainforest habitats in Australia and New Guinea, the author has never witnessed any predation on a bird of paradise, nor found any remains of such, and other observers have reported similar experiences. Perhaps they are mostly of sufficient size and mass to deter predators, and also equipped with strong and stout feet and bills which may be a deterrent. No doubt predation by raptors does occur opportunistically, as the following indicates: 'Earlier this year I experienced first hand a Black-mantled Goshawk (*Accipiter melanochlamys*) hunting for singing King-of-Saxony BoPs at the summit clearing above Rondon Ridge – fortunately we scared the bird off before it had the opportunity to make contact, but it was very clear what it was trying to do' (T. Palliser *in litt.*). Certainly when perched and calling or displaying, paradisaeids will react strongly to any passing raptor, even innocuous species such as a Whistling Kite (*Haliastur sphenurus*) or Black Kite (*Milvus migrans*), and it is likely that all the larger accipiters would opportunistically prey on them. Rand & Gilliard (1967) reported a Lesser Bird of Paradise being eaten by a Doria's Hawk (*Megatriorchis doriae*), and C. Frith (1998) has seen a Grey Goshawk (*Accipiter novaehollandiae*) take a Victoria's Riflebird. A male Black-billed Sicklebill was preyed on by what was probably an accipiter in 1974 (Pratt in F&B), but was replaced within days by a female-plumaged singing male.

Snakes, particularly pythons, must also pose a threat, and again at Kuranda it is noteworthy that Victoria's Riflebird has a particular alarm call heard only when one of the local pythons is located and is being encouraged to move off by vocal mobbing behaviour, with the riflebird always a leading protagonist. Presumably, active nests would constitute the main target at risk of predation, but again there is a lack of information. Dr Stephen Ambrose (*in litt.*) commented as follows: 'I wonder if predation is that common? In forests and other dense vegetation where brightly coloured birds are found, there would be dimmed ambient light, particularly close to the ground. Bright colours are harder to see in low light conditions, especially from a long distance away. Conversely, there are other bright colours near the top of a forest canopy, e.g. fruits and flowers, so bright coloration may be an advantage under those conditions. But my overall feeling is that the usual cryptic behaviour of these birds (except when displaying) and their stealth of movement probably counter the risk of predation from being brightly coloured. There are lots of brightly coloured bird species in global tropical and subtropical forests, particularly in South America, so either bright colour doesn't disadvantage them greatly with respect to predation risk, or enough survive to breed and keep populations going.

'Reptiles do have colour vision, but I suspect that many snakes would rely more on body heat, odour and vibration to detect prey, and goannas rely more on odour, especially in dark forest situations.'

Human predation on birds of paradise has been the subject of various books over the years, such as that by Swadling *et al.* (1996), and is largely outside the scope of the current work. Suffice to say that very large quantities of plumes were taken in the 19th and early 20th centuries, for display in glass cases, in cabinets of curiosities, and as part of the millinery trade when plumes were considered desirable fashion accoutrements

**Victoria's Riflebird**, male displaying to female, Malanda, Queensland, Australia (*Martin Willis*).

by wealthy women. 'The aim of every ordinary collector… seems to be… to see how many of these beautiful creatures he can procure for the decoration of the hats of the women of Europe and America' (Sharpe 1898). Employees of the German New Guinea company had shot all the fully plumed males of '*Paradisaea (minor) finschi*' near the coast of German New Guinea. Sharpe writes that this taxon is 'so rare in museums that we may yet be compelled to study its characters by permission of our wives and daughters, whose hats are decorated with its mutilated bodies'. Most of the very rare named hybrid varieties were also derived from the plume trade: to give an idea of the scale involved, from 1905 to 1920 as many as 30,000–80,000 bird of paradise skins were exported *annually* to the feather auctions of London, Paris and Amsterdam. There is currently a somewhat worrying resurgence in the trading of plumes and skins to certain overseas destinations, and a disturbing indication that some of the Asian markets may be acquiring a taste for such beautiful, unusual and valuable status objects, with potentially very harmful outcomes. It is to be hoped that the relevant customs authorities can crack down on it. Happily, foreigners in Papua New Guinea at least are supposed not to purchase the skins or plumes, and most visitors seem to abide by the rules.

Within New Guinea, certain species are still highly prized as cultural adornment (or *bilas* in Tok Pisin language) for ceremonies, shows and sing-sings. A visit to the Mount Hagen, Wabag or Goroka shows will reveal hundreds of skins and plumes being worn for these major ceremonies. Commonly used items include the plumes of Lesser and Raggiana Birds of Paradise, the iridescent triangular blue breast shields of the male Superb Lophorina, which are in great demand as a centrepiece for head or chest ornaments, and the long tail plumes of Princess Stephanie's Astrapia, used in the spectacular head-dresses. The tail plumes of the Ribbon-tailed Astrapia and the male Black Sicklebill are also highly prized and expensive to purchase, as are the head plumes of King of Saxony males and, less commonly, the plumes of Greater and Blue Birds of Paradise or the head wires from Lawes's Parotia.

When such skins were harvested by means of traditional hunting methods the take would have been relatively small, but the advent of shotguns and perhaps even mist nets has seen the quantities rise. Without local regulation the adult males can be eliminated quite quickly, but certainly in some areas the catch is restricted, and the species concerned seem to survive quite well so long as the habitat is intact, a kind of sustainable harvest.

**Daily routine maintenance activities** have been little documented. All three species of riflebird in Australia are known to drink and bathe at pools in the forest, the Paradise and Victoria's Riflebirds using knotholes holding rainwater. A Paradise Riflebird was seen to utilise a garden pool during a period of drought, ceasing to visit when the rain returned, and Victoria's Riflebirds at Kuranda regularly use the birdbath for bathing and drinking during the drier periods. The Black-billed Sicklebill has been noted to rain-bathe at Mount Missim, sitting 10m up in a sapling and preening for some eight minutes in a heavy downpour (Beehler in F&B), while solitary males have been seen bathing in small pools (Pratt in F&B).

Preening is likely to follow bathing, the birds readjusting their plumage after getting wet. Hunters in New Guinea will wait by forest pools to snare or spear paradisaeids, both for food and for their plumes, and more recently photographers have erected hides by such sites in order to obtain remarkable photographs and videos. Some paradisaeids occupy prominent perches early in the morning, both for display purposes and, probably, to catch the morning sunlight.

**Roosting behaviour** of the family is also very little known and primarily anecdotal or based on incidental observation, although finding roosting birds in the dense forest habitat is a very difficult task. It is reported that male Wallace's Standardwings will roost above their leks, and Twelve-wired Birds of Paradise appear to roost relatively low down.

## Food and foraging

Paradisaeids have an unusually diverse range of body sizes and bill shapes, far more so than the bowerbirds do, and this reflects a quite wide range of dietary strategies. Most species are frugivorous and will also take arthropods, although a few, such as the Black-billed Sicklebill and the Superb Lophorina, are primarily insectivorous. The frugivores tend to range more widely in search of fruiting trees, shrubs, vines and plants, undertaking much foraging in the canopy of such trees. Many species are non-territorial, or defend only their display site, whereas many of the more insectivorous species maintain all-purpose territories as befits their more sedentary lifestyle.

Frugivores tend to occur more in small groups or in foraging flocks, while insectivores are more solitary, probing and gleaning for prey in bark and foliage in the forest canopy or middle stratum. The long decurved bills of riflebirds allow for probing in rotten wood, and sicklebills use theirs to probe among pandan leaves. There is also some opportunist supplementing of the diet with the taking of small vertebrates such as frogs and skinks, and also flowers and nectar. Several species are known to eat leaves, too, in captivity, and this may well be an occasional habit in the wild.

Much of the foraging for fruit is carried out solitarily, but many species will join in mixed-species bird flocks, although, when feeding from fruiting trees, they show little interaction with other frugivorous species such as bowerbirds, fruit-doves (*Ptilinopus*) or satinbirds. Unusually, a few frugivorous paradisaeids will defend a fruit source, resting and feeding by it for much of the day. Dietary preferences are still not very well known and, despite the availability of hundreds of different types of fruit, it appears from some studies that each paradisaeid species eats the fruit of only a few of the potentially available plant species. This varies according to species, some, such as the Trumpet and Crinkle-collared Manucodes, being obligate eaters of figs (*Ficus*) over much of their range, whereas other species prefer drupes or berries (Lawes's Parotia) or capsular fruits (Raggiana and Magnificent Birds of Paradise and the Superb Lophorina).

Unlike bowerbirds, paradisaeids use their feet for holding and manipulating foods, extracting the nutritional content from fruit if it is not swallowed whole. They generally pluck fruit when perched, rarely while in flight, and are among the most significant dispersers of fruits/seeds in both Australia and New Guinea. They do not digest seeds, which pass unharmed through the digestive tract, maybe even deriving some benefit from being excreted among ready-made fertiliser. The only other avian family in Australia and New Guinea with anything like this number of seed-dispersers is that of the pigeons and doves (Columbidae).

None of the paradisaeids is exclusively insectivorous, as even the primarily insectivorous ones take some fruit. A great range of arthropods is preyed on and no doubt the full spectrum will prove to be even wider, but it includes caterpillars, beetles (Coleoptera) and their larvae, katydids (Tettigoniidae) and other Orthoptera, cockroaches (Blattidae) and ants (Formicidae). Three foraging strategies are used by paradisaeids when taking such prey, namely bark-gleaning, the probing and tearing of dead wood and foliage, and the more generalised gleaning of twigs and foliage; the last of those, more generalised gleaning, is somewhat oddly more characteristic of the rather large manucodes. Foraging is done by hopping while searching foliage, boughs and tree trunks, checking dead leaves, bark and epiphytes; mossy clumps are torn into and pulled apart, bits of moss flying about as the birds probe vigorously. Most birds of paradise utilise their feet to hold prey in order to tear the item apart, but manucodes employ a different and more generalised strategy of upright gleaning among twigs and foliage, quite unusual for species as large as these.

Riflebirds are noteworthy for occupying a niche analogous to that of certain woodpeckers (Picidae), a family which is absent from this region. They cling on to trunks and branches with their powerful feet and claws, using the long, strong and decurved bill to probe and tear bark and dead wood, often delicately. They will also use the partially opened bill to probe into soft wood or debris, a technique known as *Zirkeln* (a German word meaning 'to measure with a pair of compasses'). Black-billed Sicklebills have been seen to employ their narrow sickle-shaped bill to probe into wormholes and knotholes, at times opening the bill wide and using just the lower mandible in order to spear prey, a neat adaptation with the curious slender, decurved bill.

Most paradisaeid genera will regurgitate food into the bill before swallowing it again or feeding it to their offspring. They will also regurgitate seeds and simply drop them, another facet of their role as seed-dispersers. An opportunistic feeding association occurs when pigeons and doves forage for seeds dropped or excreted near the display courts of parotias or Magnificent and Wilson's Birds of Paradise, also cleaning up the area at the same time.

As with some bowerbirds, it appears that paradisaeids will vary the dietary content fed to their young, initially provisioning the chicks with the much more protein-rich and presumably calcium-rich arthropods rather than fruit, which becomes more significant later. Arthropods form a rich dietary supplement helpful for growth and successful development, which can be met with a more fruit-based diet later once the formative stages are past. An unexpected finding from a study of the breeding biology of Trumpet Manucodes was that they seem to be obligate fig specialists at this stage, feeding the young very large quantities of relatively low-nutritional-value figs.

It is widely accepted that a frugivorous diet based on abundant and readily available fruit resources permits the adoption of polygyny as a breeding strategy, freeing the males from nest duties and permitting promiscuity and the evolution of court- or lek-based lifestyles, where the females are the primary drivers of mate choice. Recent fieldwork has focused on dietary ecology and specialised frugivory in the evolution of such complex and elaborate breeding systems, where it would appear that females require a richer diet with many more arthropods when nesting, while the males can minimise foraging time, and therefore maximise display time, by being primarily frugivorous.

## Breeding

With the exception of a handful of better-studied species, the breeding cycles of birds of paradise are still relatively poorly known, but across their range it is evident that nesting ideally coincides with a peak in the availability of fruit and arthropods. Nesting has been reported in every month of the year, with a peak from August to January and least activity in March–June, often peaking at the end of the wetter months but with great local variation depending on the differing microclimates and habitats available.

All the manucodes and paradise-crows are believed to be **monogamous**, and the sexes are alike. The pair-members share nest duties and do not maintain defended territories, as they are frugivorous and need to forage widely.

The remaining 35 species of bird of paradise are **polygynous**, all of them being sexually dimorphic, usually (except for *Paradigalla*) to a quite marked extent. The females alone perform the nest duties, while the males are focused wholly on display and courtship, spending the maximum possible time at their courts in order to increase the chances of successful mating. These promiscuous males use traditional sites year after year. Display sites range from branches in the forest canopy or understorey to vertical tree trunks or stumps, vine tangles, fallen logs, or the more elaborate terrestrial courts or dancing grounds of *Parotia* and the *Cicinnurus* species, which are cleared by the birds themselves. Males of many of the polygynous species modify their display sites by removing leaves growing around the immediate area, this gardening thus improving visibility and sight lines for spotting not only potential mates but also rivals and predators, making the site more obvious and enhancing lighting conditions, which are important for optimum views of the plumage.

The individual species' displays are described in some detail under each species account, as are nesting details in so far as these are documented. Numerous gaps remain, with the nests of several species still undescribed at the time of writing; for example, the nest of the Arfak Astrapia was first found in 2017, while the nests of the Black Sicklebill and Wilson's Bird of Paradise remain unknown. For nearly half of the other species, including such widespread ones as the King Bird of Paradise, the Twelve-wired Bird of Paradise and most of the parotias, only the barest details of nests and eggs are known.

Some recent discoveries have been made concerning iridescence and the role of ultraviolet in paradisaeid displays, the colour blue in particular being potentially very significant, but this is as yet little known. It may be that females have a particular preference and adult males with the greatest UV reflectance may be at an advantage compared with immatures, which lack or have much-reduced UV coloration. The iridescent blue/magenta/violet tips of the breast-shield feathers of sicklebills and astrapias, some of which display in fairly dim light, may have unexpected dimensions in how they are perceived. It is now realised that the bright white narial shields of the parotias and the extraordinary head pattern of Wilson's Bird of Paradise are very striking when viewed from directly above, as happens when the females are watching the males display on their courts. The various head wires and long, curved iridescent rectrices are also fantastic signalling devices, and it would be good to know more precisely how these are perceived by the females.

Another recent study (McCoy 2018) has revealed that the structure of paradisaeid feathers is very distinctive, with myriad tiny protrusions that stick up with no exposed flat surfaces, unlike the usual black feather structure, which has flat surfaces that reflect varying amounts of light. These protrusions combine to absorb 99.6% of direct incident light, which means that the black feathers of paradisaeids such as riflebirds (and presumably *Lophorina* and *Parotia*) are the blackest of the black (the blackest material so far known has an absorption rate of 99.6%). This has implications for the displays, as the contrast with the coloured iridescent feathers is thus greatly accentuated, making the males even more striking to the females. Quite what this means with the entirely black manucodes, and whether their feathers are structured in the same way, is not yet known. As always, one line of research opens up yet more lines to be explored.

There is great variety in the display strategies of the polygynous species, these ranging from solitary and non-territorial displays through a range of intermediate strategies to true communal lekking. Solitary and non-territorial display is the most frequently used, with considerable variation even within that: Magnificent and Wilson's Birds of Paradise and the parotias use cleared terrestrial display courts, while the *Ptiloris* riflebirds display from a simple tree snag or branch. Most solitary species display in the understorey, but a few, such as the Twelve-wired Bird of Paradise, use prominent perches high above ground or, as in the case of the King of Saxony and Blue Birds of Paradise and the lophorinas, sing from exposed perches and display much lower down.

Those species which display solitarily have greater space between their territories, thus minimising or avoiding rivalry but often within auditory contact of competitors, as with the Twelve-wired Bird of Paradise. Their display periods tend to be quite limited, with less time spent displaying compared with the court-based species, often with a short early-morning display and frequently a repeat later in the afternoon. The Twelve-wired Bird of Paradise at Kiunga typically spends around 20 minutes in the early morning on the display perch, and has finished at around 07:00 hours, but much depends on female activity. This type of courtship by solitarily displaying promiscuous males, such as those of riflebirds and the Twelve-wired Bird of Paradise, includes sudden advances at females, sometimes buffeting them with the wings, pecking at them, changing size and shape by erecting various plumes, showing off colourful bare parts such as mouth-linings, legs or even the bare thigh patches in this latter species, and using different vocalisations.

In an interesting variation, males are loosely clustered over a wider area and in auditory contact with one another in what is termed an 'exploded lek'. The strategy used by the King Bird of Paradise is a good example of this, with two to four males situated 50–70m apart. Both Lawes's and Carola's Parotias seem to behave similarly at some sites.

The species that form what can be termed true leks include Princess Stephanie's Astrapia, Wallace's Standardwing and most of the *Paradisaea* species, while up to five male Ribbon-tailed Astrapias have occasionally been seen together in some form of display association. These leks vary in the numbers of individuals involved, which can range from just a couple to more than 40 in the case of Wallace's Standardwing and the Raggiana Bird of Paradise, all in close proximity in a single or sometimes several tall trees. Leks tend to be scattered and can be a few hundred metres or a kilometre or more apart, but much depends on the habitat, population density, levels of disturbance and hunting pressures, with many formerly large leks now sadly much depleted. Some of them have been in existence for many years, with one lek of Greater and Raggiana Birds of Paradise at Kiunga active for more than 20 years from March/April through to October/November, but again this depends on many variables.

There is fierce competition among the males at the leks, the older birds generally having dominance and getting what may be termed the prime or alpha positions for attracting females for successful mating. Much squabbling goes on, with chasing and pecking, and with great vocal interplay among the males of the various age classes, all coupled with attempts to lure females at the same time. Studies suggest that older leks have more males, less territorial aggression and more female visits, the converse holding for newer, smaller leks, which have more fights between males and fewer visits by females. A distinctive and unique feature within these leks is the existence of a **convergence display**, whereby males will suddenly and noisily arrive or converge as females show up.

Polygynous species advertise their presence by means of their colourful plumage and loud calls, but the type of display which they have evolved will depend on the sort of perch which they utilise. The terrestrial-court species have elaborate and complex ritualised dances involving astonishing shape transformations, as does the Superb Lophorina using a log or bare ground, whereas the King of Saxony simply bounces up and down on understorey vines. Those species using vertical snags have much more limited and static repertoires. Such species will drastically alter their shape by erecting flank plumes or breast shields, and zigzag up and down (Twelve-wired) or sway rhythmically back and forth (Black Sicklebill), or form a striking fan shape with swishing noises as Victoria's Riflebird does. The congeners of the last-mentioned species have a much more linear hopping format, still forming a wing-fan with associated sounds but on horizontal limbs or thick vine stems, rather than a display post.

The more complex and ornate the plumage, the more complex and elaborate the display may be a good generalisation in this family, which also has probably the most extreme examples of sexual dimorphism. For each specially modified feather, be it plumes of varying sorts, erectile fans, wing feathers or tail feathers, there is a corresponding ritualised display pose. For example, the King of Saxony waves his flashing head plumes, erects his mantle cape and vibrates the wings to show the pale buff patches. Black Sicklebills erect the axe-shaped epaulettes on the shoulders and flash the iridescent feather tips while swaying rhythmically and showing off the large size and long tail, whereas astrapias have specific poses which show their long tail to great advantage. It is hardly surprising that many of the historic illustrators got the poses of the birds completely wrong!

There is a strong auditory but non-vocal component to some displays. The riflebirds, for instance, show off their specially modified wings, which make a swishing sound when hoisted into the fan shape, and the Superb Lophorina produces curious clicking sounds by rapidly opening and closing its wings in display. The wings are quite prominent in many of the *Paradisaea*, which hold them in specific striking poses, flutter them and also make sounds by striking the carpal joints together while displaying. Wallace's Standardwings also strike their carpal joints together to make quite loud cracking or snapping noises, a louder sound than the *Paradisaea* produce. Bill-rattling is known from Pale-billed Sicklebills during courtship, and riflebirds are well known for the rustling plumage of the males which, when displaying, produce loud swishing noises with the wings as well as wing-beating the female. Male astrapias are similarly very noisy in flight, making loud rustling sounds, and some incorporate elements of wing noise into their displays.

Scholes *et al.* (2017) produced a fascinating and important paper on the displays and courtship of the genus *Astrapia*, derived from detailed analysis of the audiovisual material lodged with the Cornell Lab of Ornithology. They state that the behavioural components of courtship for species in the genus *Astrapia* are very poorly known (Healey 1978; F&B 1998; Laman & Scholes 2012). There is no inventory of systematically named and described courtship behaviours or vocalisations for species in the genus. Summaries from species accounts in the secondary literature indicate a few simple behaviours, including a form of hopping back and forth between branches and an inverted display posture by the Huon Astrapia (Healey 1978; F&B 1998; Frith & Frith 2010).

One remarkable display, the **inverted tail-fan display** of the Huon Astrapia and Arfak Astrapia, is one of the most distinctive and specialised of all the *Astrapia* courtship behaviours and, indeed, of all paradisaeid displays. In this family, true inverted displays – i.e. those that involve hanging upside-down from a horizontal branch – are known for only three species from the *Cicinnurus–Paradisaea* clade: the King Bird of Paradise, the Blue Bird of Paradise and the Emperor Bird of Paradise (F&B 1998; Laman & Scholes 2012). Several other species adopt head-down inverted postures from vertical or sloping branches (e.g. Twelve-wired Bird of Paradise and Greater Bird of Paradise), but they do not hang fully inverted in the manner of those mentioned above and the two species of *Astrapia*.

The overall similarity of the inverted displays of Huon and Arfak Astrapias is quite striking, and such strong convergence in display behaviour is uncommon even among paradisaeids in the same genus. The parotias are an example: even though the **ballerina dance display** is shared by all the species in the genus *Parotia*, the details of the displays are nevertheless different, with diagnosably distinct components, for each *Parotia* species (Scholes 2008c). Because data documenting the inverted tail-fan display of the Arfak Astrapia are so few and likely incomplete, we feel confident that there are additional components still to be discovered which will distinguish it from the inverted display of the Huon Astrapia. These differences are likely to be most noticeable in displays given to females, which is something that has not yet been documented for the Arfak Astrapia.

Both the Huon and the Arfak Astrapias have highly iridescent abdominal plumage, which appears dark (almost black) when the birds are in normal upright perched posture. When the abdominal feathers are oriented skywards during inverted display, however, they become highly visible, another notable feature of the displays of these two species. Interestingly, the Splendid Astrapia has highly iridescent green abdominal plumage, which raises the question of whether it, too, has an as yet undocumented inverted display. According to the best-supported recent phylogeny available, *A. nigra* and *A. splendidissima* are sister-species, the two together being sister to a clade that includes *A. rothschildi*, *A. mayeri* and *A. stephaniae*, with *rothschildi* as the basal member (Irestedt *et al.* 2009). This means that the possession of green abdominal plumage is likely to be ancestral and that the darker abdomens of *A. mayeri* and *A. stephaniae* are derived. It further implies that the inverted-display behaviour either evolved twice, independently, in *A. nigra* and *A. rothschildi* or that it is also, like green abdominal plumage, the plesiomorphic state and was present in the common ancestor of the extant *Astrapia* clade. If the second scenario is true, we can predict that *A. splendidissima* is likely have an inverted courtship display similar to those of *A. rothschildi* and *A. nigra*. Documenting the presence of or confirming the absence of an inverted display in *A. splendidissima* should be a high priority for future field observers (Scholes *et al.* 2017).

Mouth-lining colour is also quite vivid and significant in many species of paradisaeid, ranging from bright orange or yellow to lime-green and shown prominently when the bird is calling, though seemingly not with *Paradisaea* or Wallace's Standardwing. Leg colour, too, may be utilised in visual displays, *Cicinnurus* having bright blue legs, Twelve-wired possessing colourful reddish-pink legs and thighs, and Wallace's Standardwing exhibiting orange-yellow legs.

Inverted display poses are used by several species, including *Paradisaea* and *Astrapia*. Especially noteworthy is the Blue Bird of Paradise, which hangs upside-down and flashes the iridescent breast markings while making an amazing pulsing 'electronic' sound, *kisim pawa* ('go electric') in the local Tok Pisin tongue. The Emperor

**Wallace's Standardwing**, male at lek, Halmahera, North Maluku, Indonesia (*Chien Lee*).

Bird of Paradise differs not only vocally, but also in holding the wings open when inverted and flashing the deep green breast colour and white flank plumes. The King Bird of Paradise is one of the most remarkable of all, swaying backwards and forwards like a pendulum, resembling a glistening red tomato in a gale, when inverted. Other strange adaptations are the bare bright blue head skin of both sexes of Wilson's Bird of Paradise, elongated tail wires that are very obvious in the *Paradisaea*, and the flank wires of the Twelve-wired Bird of Paradise. The male of this last-mentioned species uses these wires to brush the face of the female, an unusual tactile element of the display, but the function of the elongated central rectrices of the *Paradisaea* is not known beyond the visual effect of the long, twisted shiny black ribbons of the Red Bird of Paradise. The Blue Bird of Paradise, in the monotypic genus *Paradisornis*, also has long central rectrices, the tips of these with iridescent mirror-like blobs which bob and sway.

None of the paradisaeids is known to be a colonial nester, and none has helpers at the nest, while almost all known nests have been built in branches of varying tree species. Some, such as Victoria's Riflebird, the Trumpet Manucode and the Twelve-wired Bird of Paradise, nest in the heavily foliaged crowns of small saplings, palms or pandan-type species, where there is some protection from arboreal predators such as snakes. The Trumpet Manucode may have a nesting association with the Black Butcherbird (*Melloria quoyi*) on Cape York, at least, the manucode building its nest near that of the predatory butcherbird, although how it avoids having its own nest preyed on remains unknown.

Both of the smaller Australian riflebirds are known to build sometimes atop the previous season's nest or at least nearby, and use a traditional site, and the same holds true for the Short-tailed Paradigalla (*Paradigalla brevicauda*) and Ribbon-tailed Astrapia, at least. Whether the same male is the parent is not known, but it must be a strong likelihood given that the same display sites are used year after year.

There are two basic types of **nest structure** within the paradisaeids, none of which is known to use sticks in its nests, a very different situation from that of the bowerbirds, where sticks are commonly used. The more ancient basal group of manucodes and paradise-crows builds shallow open cups of mainly vine tendrils, sometimes with a lining of dead leaves or dead wood, these being constructed in a branch fork. All the other known paradisaeid nests are deep and bulky bowls of orchid stems, leaves, mosses and ferns, also built in branch forks. An unusual and well-documented habit in Australia is that the females of both Victoria's and Paradise Riflebirds typically decorate the nest rim with sloughed snakeskin, which may perhaps deter some potential predators.

Data on the **clutch size** of birds of paradise are limited, but clutches typically consist of one or two eggs (rarely three), laid on consecutive days, although the monogamous manucodes typically have two-egg clutches (rarely three) and this may reflect the greater time available for foraging and provisioning nestlings when both sexes perform nest duties. Interestingly, what little is known of the highland paradisaeids seems to indicate that single-egg clutches are the norm, perhaps reflecting the poorer availability of food in the cooler, damper climates – although this, of course, conflicts with ideas about the diversity of species here being due to a greater variety of foods. So much remains to be learned. Data on the eggs of paradisaeids and brief egg descriptions are given under each species where known.

**Incubation** periods are known for only some of the polygynous species of this family, and range from 14 to 27 days, the longer periods occurring at higher altitudes. Passerines typically spend 60–80% of each day incubating, and this holds true for both polygynous species and those in which both sexes incubate so far as is known. Unlike the downy pale-skinned young of bowerbirds, paradisaeids hatch naked or with only very sparse down and they have, or develop, dark skin.

**Nestling or fledging** periods are known for only a few species and vary from 14 days to 30+ days; as with incubation, they seem longer for higher-altitude species than for lowland ones. The eyes open at around six days of age, and at about 8–10 days the body feathers of *Paradisaea* nestlings emerge from the pin tips, the primary coverts and primaries emerging at about two weeks of age. Frith *et al.* (2017) state that 'Growth curves for nestling birds-of-paradise in the wild show that the larger species grow at a fast rate, and also that all such curves are virtually linear over much of their length, except for the downturn just prior to the chicks' departure from the nest. Nestlings regularly lose some weight at this time because of the energetic cost of rapid growth of the tail feathers and flight-feathers.'

Data on **nest-provisioning** and nestling-brooding are scant. Females can spend anything between 14% and 48% of their time in brooding young, but much may depend on weather conditions, food availability, the physical condition of the female, and so on. Similarly, and again subject to many variables, feeding of single-chick broods varies from one to three meals per hour, while Trumpet Manucodes feeding two young over four days averaged 3.4 feeding visits per hour.

Paradisaeids, unlike bowerbirds, feed their young by regurgitation, the exception to this being that sometimes a last item is carried in the bill and fed directly to the chick. The faeces of the nestling seem to be swallowed, although this behaviour is as yet poorly known, and they may be carried away from the nest late in the cycle as fledging becomes imminent.

**Distraction displays** and aggressive nest defence occur but are very little known. Females will chase away conspecifics that venture into the general nest area, and Victoria's Riflebird and the Raggiana Bird of Paradise simply 'freeze' on a perch at the sight or sound of a potential predator.

Information on **parental care** once the young have left the nest is very limited. Juvenile Victoria's Riflebirds are certainly fed by the female for some weeks after fledging, and one timed instance was up to 74 days. A female Short-tailed Paradigalla was seen to feed an immature for as many as 108 days, but she apparently ceased doing so a week later.

**Nest parasitism** is very rare, the only documented example being of an Eastern Koel (*Eudynamys orientalis*) that laid an egg in an active nest of a Victoria's Riflebird, but the hosts for many of the New Guinea cuckoos are remarkably poorly known.

## Voice

Birds of paradise are among the most spectacular avian species in the world in terms of plumage and displays, but their vocalisations are not quite in the same league. Many make loud, harsh sounds vaguely reminiscent of the calls of corvids, but none has anything that can be described as a conventionally beautiful song. Unusually, both sexes of the monogamous species, the manucodes and paradise-crows, call regularly, the Trumpet Manucode having sex-specific notes. Conversely, among the polygynous species, it is typically only the males that vocalise, giving loud and often far-carrying advertisement calls. The females appear to be largely silent except when alarmed, although the picture is complicated by the fact that young males have female-like plumage for some years and are quite vocal, rehearsing their repertoire for later.

Some truly extraordinary sounds are made by paradisaeids. One of the most unusual is the bizarre and electronic-sounding pulsing intense-display call of the male Blue Bird of Paradise, given while the bird is hanging upside-down in a dense thicket, and quite distinct from the sonorous bugling of the advertisement call, which carries up to 2km across the mountain valleys. The King of Saxony Bird of Paradise, as well as having one of the longest vernacular names, has a very strange fizzing rattling series, given by the males on their songposts, while the Brown Sicklebill is famous for the loud machine-gun-like rattle produced by the males. Other odd calls are emitted by manucodes, the Trumpet Manucode somewhat imaginatively named for trumpeting its advertising call, the Glossy-mantled having a rising call resembling the sound made by a tuning fork, and some manucode species having quiet deep sonorous calls which may have an infrasonic element that helps the sounds to carry through dense forest habitat, a field that merits research.

When properly courting, as opposed to advertisement calling, males of the plumed *Paradisaea* species are relatively quiet, some species making sharp clicking sounds with their mandibles or giving just a few brief soft notes. Magnificent Birds of Paradise also give soft, quiet contact notes when courting, and make a similar clicking sound, while Wallace's Standardwing emits quiet twittering noises in display and the King of Saxony utters much quieter vocalisations when bouncing up and down while displaying on a vine.

There are no convincing records of **mimicry** by birds of paradise in the wild, in complete contrast to the bowerbirds, which are famous for it. Some quiet *chip*-type notes may resemble those of other species but are not convincing demonstrations of mimicry. Some examples published on websites have proven to be misidentifications of different species, and it is essential that, for a convincing record, the bird must be seen to be producing the sound.

## Movements

The birds of paradise are a little unusual in that there are no migratory species in the family. All are basically resident and sedentary, with some very limited and local dispersal in relation to food abundance or scarcity, drought or fire. In Australia, both Victoria's and Paradise Riflebirds undertake some dispersal into adjacent drier woodlands after breeding and in winter, the latter species being known also to wander down to the coastal lowlands in winter, but otherwise occurring at elevations above about 200m. Victoria's Riflebird similarly has some limited dispersal to drier woodlands west of the Great Divide, but there are no records of vagrancy as such for any of the family.

## Conservation

New Guinea still has a great abundance of forest, much of it in extremely challenging terrain, and this has thus far enabled many of the island ecosystems to remain relatively intact. Hunting has been continuous for thousands of years, formerly at low-impact and largely sustainable levels until the advent of modern technology and the vastly increased human-population pressure adversely tipped the balance.

Timber extraction remains a major threat, with the consequent degradation/devastation of the forest, while wholesale replacement of lowland-forest ecosystems with oil-palm (*Elaeis guineensis*) monocultures is a developing problem in certain parts of the mainland lowlands. Copper- and gold-mining has also adversely affected substantial local areas, with gas extraction the latest extractive industry to have an impact, opening up previously remote and inaccessible areas to exploitation. The rapidly expanding human population is also a mid-term problem, with around 2% rates of annual increase very fast and exerting increasing pressure on fragile resources.

National parks, which might offer some degree of protection, are problematic in New Guinea (and Melanesia in general), since traditional modes of land ownership render government actions in establishing national parks either impossible or largely irrelevant. Local communal decision-making in Papua New Guinea, at least, makes centralised direction difficult. Despite this, there are three quite large national parks designated in West Papua. The largest, the Lorentz National Park, dates from colonial times and extends from the Snow Mts to the Arafura Sea. Teluk Cendrawasih, in the lowland coastal Vogelkop, is largely irrelevant here as it is essentially a marine reserve. The third, Wasur, in the Trans-Fly, protects the lower Trans-Fly drainage. There are 30 other designated reserves scattered about the western half of the region, but once again many of them for marine areas or islands. Where the local community is involved in the running and maintaining of them, Wildlife Management Areas in Papua New Guinea seem moderately effective. Changing demands, expectations or local conditions, however, mean that they are not necessarily the answer in the long term.

Ecotourism is in its infancy and income generated from it is so far low and at subsistence levels, although some initiatives are quite meaningful at a local level. Much can be done to expedite wildlife-based tourism, be it centred on birds, tree-kangaroos, fish, plants or butterflies. As a result of these initiatives, increasing numbers of local people are working as skilled and knowledgeable guides. This not only directly helps the individuals involved, but also gives an important local voice to environmental concerns. The training of a cadre of guides, by aid organisations and the international conservation groups, has great potential for the future.

The great unknown with conservation these days is, of course, the impact of climate change, which can be expected to be very significant in the medium to long term. This is of particular concern for the higher-altitude species that have a restricted habitat, as it is likely that changing wind, temperature and rainfall patterns will gradually modify the flora and fauna of the forest communities, with huge impacts on all species. The potentially increased frequency and intensity of cyclones will also have serious consequences, especially for species on islands, where habitats are limited and thus very prone to catastrophic-event damage. Species at higher altitudes are likely to find their habitats shrinking, while changes to salinity, sea-level rises and vegetation modification will have adverse impacts on coastal and island species. Immense and profound changes to ecosystems can be expected over the short term, with worrying conservation implications for specialised or restricted-range species.

In Australia, all the higher-altitude rainforest taxa must be at risk as they have nowhere else to which they can relocate, and species such as the Golden (*Prionodura newtoniana*) and Tooth-billed Bowerbirds (*Scenopoeetes dentirostris*) could therefore be in trouble. In New Guinea, the Fire-maned Bowerbird (*Sericulus bakeri*), Archbold's Bowerbird (*Archboldia papuensis*) and both Long-tailed Paradigalla and Arfak Astrapia are species with restricted high-elevation ranges that are potentially vulnerable. Much depends on the next few years, but the overall prognosis has to be bleak, with political will lacking and vast socio-economic pressures driving development irrespective of environmental costs, which are never included in the economic-cost packages.

All members of the paradisaeid family in Australia are classified by BirdLife as being of Least Concern (**LC**), with none currently rare or endangered. In New Guinea, on the other hand, the picture is not quite so rosy, this due primarily to habitat loss or damage coupled with some small-scale hunting for certain highly prized species:

**VU** Vulnerable: Black Sicklebill, Blue Bird of Paradise and Goldie's Bird of Paradise

**NT** Near Threatened: Wahnes's Parotia, Pale-billed Sicklebill, Long-tailed Paradigalla, Ribbon-tailed

Astrapia, Wilson's Bird of Paradise, Emperor Bird of Paradise, Red Bird of Paradise. All of these are of relatively restricted range and several are island endemics.

Membership of conservation organisations is becoming increasingly important as the human population inexorably rises and the 'Great War' on nature intensifies. There is a continuing loss and degradation of forest habitats even in such relatively prosperous countries as Australia, and far worse in both Papua New Guinea and Indonesia, the other states having custodianship of these two spectacular families. Important organisations that have achieved significant conservation outcomes are BirdLife International, based in the UK and with regional branches in Australia and Indonesia, and Conservation International from the USA, which has done a great deal of conservation work with ecologically sound credentials and centred on local people in Papua New Guinea.

The BirdLife affiliate *Burung Indonesia* has some worthwhile goals, which neatly encapsulate conservation aims in the context of that important country for birds of paradise and bowerbirds. Its mission statement is as follows.

## Aim

- To be the guardian of Indonesia's wild birds and their habitats through working with people for sustainable development.
- To achieve this, Burung Indonesia has been dedicated to:
- Promoting conservation of sites, species and habitats.
- Working with communities to promote collaborative conservation and natural-resource management for sustainable development.
- Developing the organisational capacity for improved management of habitats, sites and species.

## Key activities

- Comprehensive conservation action for species, sites and habitats through working in protected areas, sustainable productive landscape management and ecosystem restoration in production forests.
- Policy advocacy at local and national levels, utilising multi-stakeholder approaches.
- Research and monitoring work on priority bird species (globally threatened, endemic, or species of parrot) in the Wallacea region.
- Management of data, information and knowledge to set priorities, support conservation actions, and function as a provider of information services to external constituencies.
- Public involvement through local conservation groups, membership of as well as working with the media, NGOs, individuals, and private-sector and government agencies.
- Promotion of bird conservation to the public.

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## What is a bowerbird? The family Ptilonorhynchidae

Bowerbirds and the *Ailuroedus* catbirds are all members of the family Ptilonorhynchidae, and include species that build some of the most striking and complex structures in the avian kingdom. The scientific name refers to the partial covering of the base of the bill by feathers, from the Greek *ptilon* (feather) and *rhunkos* (bill). They constitute a family that currently, with the latest taxonomic adjustments, comprises some 28 species in eight genera, restricted to Australia and New Guinea. In New Guinea they live primarily in the rainforests, with a couple of forest-edge and savanna species. In Australia they occupy rainforest and drier woodland habitats. Bowerbirds and catbirds do not occur west of Wallace's Line in Sulawesi, and are also absent from Halmahera, the Bismarck and Solomon Archipelagos and parts of the arid interior of Australia.

The family is divided into two subfamilies, Ailuroedinae (catbirds) and Ptilonorhynchinae (bowerbirds), an ancient separation dating back around 24 million years (Irestedt *et al.* 2105). The molecular studies of Barker *et al.* (2004) indicated that this family is a sister-group to the Australasian Treecreepers (Climacteridae), a placement corroborated by Jønsson *et al.* (2011).

Although fairly compact, the family supports eight generic lineages in four major groups:

- **The catbirds (*Ailuroedus*) and Tooth-billed Bowerbird (*Scenopoeetes*):** All the catbird species are most obviously more closely related to one another than they are to any other bowerbirds; recent biomolecular research indicates that they diverged from other bowerbird genera about 24 million years ago, and that they are quite distinct from the builders of avenue bowers. The Tooth-billed Bowerbird is, however, as distinct from the catbirds as are other bowerbird subgroups, and appears to be genetically closer to the New Guinea *Amblyornis* gardener bowerbirds than it is to catbirds (Kusmierski *et al.* 1997).
- **The *Amblyornis* grouping, the gardener bowerbirds:** including Golden Bowerbird (*Prionodura*) and Archbold's Bowerbird (*Archboldia*) and perhaps Tooth-billed Bowerbird (*Scenopoeetes*).
- ***Sericulus* and *Ptilonorhynchus***: the avenue-bower-building silky bowerbirds.
- ***Chlamydera***: the avenue-bower-building grey bowerbirds.

The *Ailuroedus* catbirds (the Spotted and White-eared Catbird assemblages) are now classified as some ten species, after recent research revealed more of the genetic history of this cryptic group (Irestedt *et al.* 2015). This group and the Tooth-billed Bowerbird are the basal members of the family, but somewhat divergent in breeding behaviour.

These ten species of the green *Ailuroedus* catbird group all lack marked sexual dimorphism, form pair bonds in which the male helps to build the nest but only the female incubates, and have rather simple arboreal chasing displays without the use of bowers or stages. In contrast, the sexually monomorphic but polygynous Tooth-billed Bowerbird has a terrestrial display and builds a simple stage of large leaves on the forest floor as a display arena, the males not forming pair bonds and not helping to build nests or to raise the young.

Gilliard (1969) pointed out that the bowerbird species with the most beautifully plumaged males exhibit the smallest and least-developed bowers, all of the sexually dimorphic species being polygynous and bower-builders. The *Sericulus* species build fairly small avenue-type bowers with limited decoration, while the Satin Bowerbird (*Ptilonorhynchus violaceus*) builds a much more elaborate type of avenue bower, lavishly adorned with found objects (often of a bright blue colour). Members of the *Amblyornis/Prionodura/Archboldia* assemblage build some of the most remarkable structures in the avian world, the species of the genus *Amblyornis* constructing maypole-type bowers. These include the Vogelkop (*Amblyornis inornata*) and Streaked Bowerbirds (*A. subalaris*), which build a highly distinctive hut-style structure, as well as the Golden Bowerbird, which constructs a double maypole bower. *Archboldia* makes a strange mat-type formation and uses unique decorative items, including beetle wings and the plumes of the King of Saxony Bird of Paradise.

### An anomaly from New Zealand

There is one anomalous genus, *Turnagra* from New Zealand, of what are now considered to be two species, the New Zealand Thrush or North Island Piopio (*T. tanagra*) and the South Island Piopio (*T. capensis*). The piopio has been the subject of an extraordinary amount of taxonomic speculation over many years, having been variously allied with thrushes (Turdidae) and then accorded a new family Turnagridae (Buller 1887), before being placed in Corvidae, and later allied to Ptilonorhynchidae on the basis of external morphology

(Finsch 1874). Mayr & Amadon (1951) allied it with Pachycephalidae and later workers placed it with both bowerbirds and the cnemophilines, which were then considered a subfamily of birds of paradise. *Turnagra* languished as basically *incertae sedis* for many more years, but the most recent detailed genetic research now places it with Oriolidae (Zuccon & Ericson 2012) and it may be that the long uncertainty has finally been resolved.

The piopio was formerly fairly tame and common in some areas but declined rapidly in the 1880s, the last North Island specimen dating from 1902, although it was rumoured to exist right up to the 1930s or even later. The population of the South Island Piopio on Stephens Island – infamous for the eponymous flightless Stephens Island or Lyall's Wren (*Xenicus lyalli*), claimed to have been extirpated by the dreaded 'Tibbles', the lighthouse-keeper's cat – was common until 1895, but had gone by 1898, presumably a victim of the same or another noxious feline. The decline has been attributed to land clearance, the introduction of numerous feral predators and disease, although the bird was also found by settlers to be tasty eating: 'it makes a savoury broil for those who bring the right sauce – hunger' (Hutton & Drummond 1904).

## Bowerbird biology

Most of the New Guinea bowerbird species are found mainly in the hills and mountains, although five – the Flame (*Sericulus ardens*) and Fawn-breasted (*Chlamydera cerviniventris*) Bowerbirds and three of the catbirds – are primarily lowland-dwelling. All of the *Chlamydera* species (Great, Fawn-breasted, Yellow-breasted, Spotted and Western Bowerbirds) prefer non-forest drier scrub and edge habitats, but the remaining members of the family inhabit the forest interior, ranging upwards in elevation to the edge of the treeline. All are primarily frugivorous and some are fig specialists. The males of the polygamous species are noted vocalists and are adept at mimicking sounds, including the songs of other bird species and sounds of human origin.

The name 'bower-bird' was first coined in 1840 by the renowned naturalist John Gould, who had seen bowers of Spotted (*Chlamydera maculata*) and Satin Bowerbirds in New South Wales in 1839. He was talking about the very first bower ever seen in England, that of a Satin Bowerbird, which was exhibited at the Zoological Society of London. Gould saw a structural resemblance to a wooded bower, which in formal landscape gardening at that time was a romantic secluded trysting place with a seat. The name has been used ever since to cover the great variety of bowers constructed by most species of the family.

The majority of bowerbirds are stout-bodied and lack a long tail, are primarily frugivorous, the males build varyingly complex bower structures, and the female alone constructs the nest and carries out the incubation and nestling-care duties. The exceptions are the *Ailuroedus* catbirds, which are monogamous, share some of the nest duties between the sexes (though the female incubates the eggs) and do not build bowers or stages, and the rather aberrant Tooth-billed Bowerbird, which makes a simple stage of upturned leaves on the forest floor but is not monogamous and does not share nest duties.

Bowerbirds were once widely considered closely related to birds of paradise, and were sometimes even combined with that family in either Paradisaeidae (Stresemann 1934; Gilliard 1969) or Ptilonorhynchidae (Sharpe 1891–98; Schodde 1975; Cracraft 1981) on the grounds of certain similarities in zoogeography, chunky body shape, sexual dimorphism and a polygynous breeding strategy. As the sum of knowledge grew, however, it was realised that major differences exist:

- Egg coloration differs between the two families.
- Eggs of a clutch are laid on alternate days by many bowerbirds, but on consecutive days by paradisaeids.
- Nestling plumage differs, that of bowerbirds being very downy and pale-skinned, not bare-skinned and dark like birds of paradise.
- Parent bowerbirds do not feed the young by regurgitation.
- Differences in skull osteology exist, an enlarged lacrymal (part of the cranium bone structure) near the eye socket being a feature unique to the Ptilonorhynchidae and the lyrebirds (Menuridae).
- Some bowerbirds are known to cache food, a trait not shown by birds of paradise.
- Many bowerbirds are accomplished mimics, another trait not found in birds of paradise.
- The loud bugling or far-carrying calls of many birds of paradise have no equivalent in bowerbirds.

- Nest structure differs between the two families, the bowerbirds (unlike paradisaeids) using a woody stick base.
- The use of bowers for display by the males is restricted to bowerbirds, whereas birds of paradise are mostly landscape gardeners rather than architects (using arenas or courts, instead of using sticks or vegetation for construction purposes).
- Elements of the displays differ greatly, and the hide-and-peek display of some bowerbirds is unknown among the paradisaeids.
- Bowerbirds include several species known to use a tool to paint their bowers, tool use being a very rare habit among birds.
- Bill size and shape are relatively uniform among the bowerbirds, lacking the great range of shape and size found in the paradisaeids.
- Birds of paradise and bowerbirds both have 12 rectrices and ten primaries, but bowerbirds have an atypically large number of secondaries (11–14 including the tertials).
- Hybridisation is very rare in bowerbirds, but much more widespread in birds of paradise.
- The bowerbirds do not use their feet to hold or manipulate food items, whereas paradisaeids are quite adept at this.

Stonor (1937) found no evidence that the two families were closely related, and classified bowerbirds as a distinct family with no close relatives. Sibley & Ahlquist (1985, 1990), in their pioneering studies of DNA–DNA hybridisation, also found that bowerbirds had no close relatives and were in fact part of the great corvoid songbird lineage. Christidis & Schodde (1991) showed a relationship with Artamidae (butcherbirds, woodswallows etc.), and later studies also reveal them as a monophyletic family (Kusmierski *et al.* 1993). Bowerbirds are a part of a major radiation in the Australasian region over the past 60 million years, diverging from lyrebirds (Menuridae) and scrub-birds (Atrichornithidae) about 45 million years ago (Sibley & Ahlquist 1985). The divergence from the other corvine lineages seems to have occurred around 28 million years ago, the main lineages of the bowerbird family evolving about 24 million years ago (Helm-Bychowski & Cracraft 1993), although these findings were based on molecular-clock calibrations, which are still being resolved.

The exact placing of the family Ptilonorhynchidae within the oscine passerines was somewhat unsettled until recent decades. The results of several biomolecular studies show it to be a highly distinctive family relatively distant from, and basal to, the Paradisaeidae within the oscines. Recent studies have shown that the majority of Australasian passerines, about 85% of the total, are derived from a southern, or Gondwanan, origin (Ericson *et al.* 2002). This major group, referred to as the ‘Corvida’, radiated in Australia and New Guinea, and today comprises three major lineages:

- Menuroidea, which includes the lyrebirds (Menuridae) and Australasian treecreepers (Climacteridae), as well as the bowerbirds; lyrebirds appear to be bowerbird relatives and are among the most ancient of the oscines (Frith *et al.* 2017).
- Meliphagoidea, which includes honeyeaters (Meliphagidae) and their allies.
- Corvoidea, which includes the birds of paradise.

The 28 species of bowerbird represent a basal group of Australasian oscine passerines, this categorisation supported by certain osteological characters such as the presence of a single corvoid pneumatic fossa (a depression or hollow) in the humerus bones of bowerbirds. Bowerbird anatomy is otherwise broadly typical of that of the higher passerines, although bowerbirds have characters of the legs, feet, palate, syrinx and spermatozoa which, in combination, can define them as a distinct family (Frith *et al.* 2017).

Catbirds are not related to the American Grey Catbird (*Dumetella carolinensis*), which is a member of the mockingbird family (Mimidae). They are, however, as with that species, named for their cat-like calls, although the loud squalling Siamese-cat-like calls of the *Ailuroedus* catbirds bear scant resemblance to the quieter raspy calls of their North American namesake. They are strongly territorial and reside in the same patch of forest year after year, using these loud distinctive calls to establish their territory (Schodde & Tidemann 1988). All the catbirds are coloured a bright leaf-green above, and have a spotted or scaled breast. The thick, short bill is pale in colour, adapted for their primary diet of fruit in their rainforest habitat. They are among the most ancient basal members of the bowerbird family and do not build bowers, which suggests that this trait evolved later. Further, the catbirds have a quite different lifestyle from that of bowerbirds, and form monogamous pairs. There are three species in Australia (one shared with New Guinea) and a further seven in New Guinea (three from the former White-eared Catbird group and four from the Spotted/Black-eared Catbird group).

These ten (formerly three) *Ailuroedus* catbird species are most obviously more closely related to one another than they are to any other bowerbirds; recent biomolecular research indicates that they diverged about 24 million years ago, and that they are quite distinct from the builders of avenue or maypole bowers. Another basal taxon is the Tooth-billed Bowerbird, which is as distinct from the catbirds as are other bowerbird subgroups and appears to be genetically closer to New Guinea gardener bowerbirds than it is to catbirds.

All bowerbirds have ten primaries and 12 rectrices, but the number of secondaries varies from 11 or 12 in *Ailuroedus* catbirds and *Amblyornis* to 12 or 13 in *Sericulus* and 14 in most *Chlamydera*. Birds occupying the more arid areas tend to be less colourful than those living in the denser forest habitats, as with the *Chlamydera* grey bowerbirds. This may reflect the greater concealment opportunities within forests and consequently the lesser need for a drab plumage. The family can be divided into three broad groupings:

- The monogamous and **non-bower-building** Spotted/Black-eared, Green (*Ailuroedus crassirostris*) and White-eared (*A. buccoides*) Catbird groups (*Ailuroedus*). The Tooth-billed Bowerbird, known also as the Tooth-billed Catbird, does not construct as bower as such, but just a simple leaf stage on the forest floor. One of the old and very appropriate names for this species was 'Stagemaker', a reference to this unique habit in the family.
- The **avenue-bower**-builders, these being the spectacularly bright-plumaged male silky bowerbirds (*Sericulus*) and the grey bowerbird (*Chlamydera*) group plus the Satin Bowerbird (*Ptilonorhynchus*).
- The third group is the largely much plainer-plumaged **maypole-bower**-building *Amblyornis* (plus *Archboldia* and *Prionodura*).

Bowerbird males display near their bower structure in order to attract females, which then choose which male they want. Males also collect display objects, the composition and quantity varying with the species, and some favouring particular colours, such as blue in the case of the Satin Bowerbird.

## Bowerbird morphology

Most bowerbirds are quite plump and stocky, with broad, rather rounded wings, and, being closely related to one another, they are morphologically less diverse than many passerine families of comparable size. They vary in body length from 22cm to 37cm, with Great Bowerbird (*Chlamydera nuchalis*) and Archbold's Bowerbird the largest, the former weighing *c.*200g. The Golden Bowerbird is the smallest, at around 80g, and unusual in being quite slender and relatively long-tailed, which makes it slightly longer than the plumper, heavier (95–140g) and shorter-tailed *Amblyornis* gardener bowerbirds. Plumage abnormalities in bowerbirds are extremely rare. The sole documented case refers to a female Satin Bowerbird exhibiting leucism, whereby the eumelanin in the plumage is incompletely oxidised and remains brown, causing a brown aberration. The aberrant bird in this case was a cream-coloured individual with bleached flight-feathers, as this mutation is prone to rapid fading (van Grouw 2012).

Typically, bowerbirds have a juvenile plumage, then a very similar immature plumage, and sometimes a distinct subadult dress before the adult plumage. Among all the catbirds, the Tooth-billed Bowerbird, the Vogelkop Bowerbird and all the *Chlamydera* grey bowerbirds the sexes are the same or very similar, and there is no distinctive immature plumage. Polygynous bowerbirds, however, generally exhibit a distinct sexual dimorphism, males of most *Amblyornis* gardener bowerbirds (except the Vogelkop Bowerbird) and of Archbold's Bowerbird having a short erectile crest of orange or yellow, this lacking in the dull brownish females and immatures. In the monotypic Golden Bowerbird the males are primarily bright yellow and greenish-yellow, whereas the females and immatures are grey-brown and whitish. The Satin Bowerbird also is monotypic, and likewise dimorphic, with a striking glossy blue-black male, while females and immatures are green above and have varying amounts of greenish scaling on the underparts. The *Sericulus* silky bowerbirds all have very striking male plumages of orange, yellow and black, the females and immatures being sombre in plumage with ventral barring.

Montane species in New Guinea are often good examples of Bergmann's Rule, which states that species resident in colder environments will average larger than those in warmer zones. Bowerbirds in both New Guinea and Australia reflect this dictum. Looking at the various genera, the upland Black-eared, MacGregor's (*Amblyornis macgregoriae*), Fire-maned and Masked Bowerbirds (*Sericulus aureus*) are all larger and heavier than their lowland counterparts in the White-eared Catbird group, the Streaked Bowerbird and the Flame Bowerbird. The bowerbird species resident at the highest altitude of all, Archbold's Bowerbird, is considerably longer than even other montane bowerbirds. The Regent Bowerbird (*Sericulus chrysocephalus*) in Australia is the largest *Sericulus* and it, too, is a hill-forest species.

Most adult bowerbirds have very similar body size and shape, but adult male Archbold's and Golden Bowerbirds develop a slightly longer tail than that of their females. The converse is true for adult female *Sericulus* bowerbirds, the Satin Bowerbird and most of the *Chlamydera* grey bowerbirds, which have a slightly longer tail than the adult males. Adult female catbirds average nearly 10% lighter in weight than the adult males, although the body proportions remain the same. Juvenile and immature bowerbirds are generally slightly smaller than the adults. Exceptions are the younger males of the *Sericulus* bowerbirds, the Satin Bowerbird and the Spotted and Western (*Chlamydera guttata*) Bowerbirds, all of which have a slightly longer tail than that of the adults. Most polygynous bowerbirds have adult females slightly smaller than adult males, except for three of the four *Sericulus* species, the females of which are the same size as or slightly larger than the adult males.

Passerines with proportionately longer legs are generally more terrestrial in habits, whereas those with shorter legs are more arboreal. Within the Ptilonorhynchidae, the grey bowerbirds in the genus *Chlamydera* have long legs, as befits their often terrestrial lifestyle, while the more arboreal Tooth-billed Bowerbird as may be expected has shorter legs.

Most bowerbirds have a relatively short, deep, robust bill, but the four *Sericulus* silky bowerbirds have a longer and finer bill. The Tooth-billed Bowerbird was for many years a puzzle, with various theories advanced to explain the unique notch or 'tooth' on both mandibles. It was eventually discovered that during winter, especially, this bird is a folivore, eating considerable quantities of leaves, and the tooth cusp and notch structure are an adaptation to help it to tear or snip off leaf pieces and wad them for consumption.

Polygynous bowerbirds generally have a dark bill, but *Amblyornis* gardener bowerbirds and *Sericulus* silky bowerbirds exhibit a pale bluish base to the lower mandible. The Satin Bowerbird has a striking bluish-white bill (which appears short owing to some feathering covering the loral area), while all the catbirds have a whitish bill with a black mouth-lining. Unlike other species in the family, adult male Regent Bowerbirds have a yellow or pinkish-yellow bill. Adult male Tooth-billed Bowerbirds have a black bill which has a contrasting white front portion on the inside of the upper mandible, whereas females and immature males of this species have the mouth pale yellowish-flesh, unlike the orange-yellow or yellow of most other bowerbirds.

Soft-part coloration is quite variable within the bowerbird family, most adults having a dark to pale brown iris, that of the juveniles being paler and greyer. Adult catbirds, however, have a red iris, which is blue-grey in juveniles, while adults of both sexes of the Golden Bowerbird have a pale iris, as do all the male *Sericulus* silky bowerbirds, though the females of the *Sericulus* species show a brownish iris. Satin Bowerbirds are very different, the males having an astonishing violet-blue iris while the females have striking blue eyes. The coloration of the legs and feet also is quite variable, ranging from black to shades of grey or olive-brown, but the Vogelkop Bowerbird stands out in having distinctly blue legs and feet.

Most male passerines develop adult plumage and breed within their first year or two of life. Males of the brightly plumaged polygynous bowerbird species, however, do not acquire full adult dress until five to six or even seven years of age. There may be a subadult plumage, with a gradual transition of some male plumage characters into the female-type dress over a year or two. Like other promiscuous male passerines that use display sites, promiscuous males of the bowerbirds have delayed acquisition of their distinctive colourful adult male features, and so can live among their conspecifics for more than five years before these become apparent.

Importantly in this family, a subadult plumage is a clear visual signal that the bird is not yet fully part of the highly competitive adult male community, although it may, of course, try opportunistically to mate with females. It is thought that a prolonged period in immature plumage may enhance a young male's opportunity to move within otherwise aggressive adult male society while gaining valuable experience. A dull plumage may also perhaps reduce the risk of attack by a predator, although predation remains remarkably little documented for either paradisaeids or bowerbirds.

## Moult

Adult bowerbirds have an annual moult, mainly during December to March, peaking during the wetter months after the young have fledged. They are in prime condition in terms of body mass and fat levels at the end of this period, just before the austral winter when it is drier and cooler and when food resources become much less abundant. The grey *Chlamydera* bowerbirds also moult towards the end of the year, after courtship and nesting, but the timing seems less clear-cut as some also shed the wing and tail feathers at other times of the year.

Detailed knowledge of bowerbird moult is available only for some Australian species, the Satin Bowerbird being quite well known, as are, to a lesser extent, the Spotted Catbird and Tooth-billed and Golden Bowerbirds. Bowerbirds follow the pattern common to most small passerines. The head-and-body moult is the most protracted, starting before that of the wings and tail but often not finishing until after the flight-feathers have been moulted. Critical flight-feathers are moulted symmetrically (presumably helping flight). Hence, the primaries in each wing are renewed sequentially from the inner wing outwards towards the tip, and this pattern is mirrored by the primary-covert moult, too. During this process the tail feathers also are renewed, starting with the central tail feathers and again working outwards (although this process is completed before the primary moult has finished). The moult of the secondaries proceeds only once four or five primaries have been fully replaced (or nearly so); in contrast, replacement of the tertials is irregular and completed before that of the secondaries has finished – see Frith *et al.* (2017).

## Bowerbird behaviour

Climate conditions and food resources, with sufficient fruit and arthropods available to sustain the heavy energy requirements of the breeding regime, are the fundamental determinants of the life cycle of the bowerbirds. Within Australia, the peak in courtship and nesting activity is primarily from late September to December (the austral spring and early summer), when temperatures and rainfall increase and food resources are at their most abundant. The start of the rains determines when the bower and nest activities finish, nestlings fledging just before or during the early wet season. This is a time of abundant resources and it is when the females, or both parents in the case of catbirds, are still feeding the nestlings. There is considerable seasonal variation in rainfall totals, even in the rainforest habitats, and in the drier country the avenue-building grey *Chlamydera* bowerbirds rely heavily on the seasonal abundance of grasshoppers (Orthoptera). Their breeding cycles are dependent upon the somewhat unpredictable rainfall. The picture in New Guinea is far less well known and more complicated, with a far greater altitudinal range and many microhabitats and microclimates making for greater variability in timing.

Behaviours known for some members of the family include the usual **preening** to keep the feathers clean and in good order, but also the less usual anting and sunning behaviour. **Anting**, using live ants (Formicidae) with which to brush the feathers, is a curious and relatively rarely observed activity of wild birds, but Tooth-billed, Golden and Satin Bowerbirds are known to indulge occasionally, and it is suggested that this may lessen parasite loads. **Sunning** is a well-known, widespread, but again still relatively mysterious and little-understood aspect of avian behaviour, indulged in by only a few of the bowerbird species. These include Spotted Catbirds and male Golden Bowerbirds, which are known to **sunbathe** by adopting a distinctive and unusual posture which resembles a sick or injured bird: they lie on the ground with the feathers of the breast, rump, head and nape erect, the tail pressed down and the wings drooped. One unusual observation was of some eight adult male and at least six 'female-plumaged' Regent Bowerbirds which sunned themselves in a semicircular area of 5m × 1.5m of open, directly sunlit leaf litter and on leafy perches above this (Frith *et al.* 2017). At any one time, up to eight of these individuals were squatting or lying on the litter in typical passerine sunning postures, this activity lasting for up to 15 minutes.

Another unusual bowerbird behaviour is the **caching** of fruits. Golden Bowerbirds conceal fruits among forest-floor litter and beneath fallen timber; these fruits, which are usually (but not always) ripe, sometimes germinate if not retrieved. Fruit-caching for later consumption is well known also for Green and Spotted Catbirds. It seems that cached fruits do not serve as bower decorations, but some male Golden and MacGregor's Bowerbirds do 'store' bower decorations around their bower sites.

Bowerbirds utilise various water sources for **drinking** and **bathing**, usually creeks and water-filled holes in trees for the rainforest species, or waterholes and cattle troughs for the grey bowerbirds of the drier habitats. Males also drink water droplets from forest-floor leaf litter and wet foliage around their bower sites. An adult