What we don't know about megapodes

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While the growth in megapode studies has been extraordinary, much remains to be done. Further work is especially crucial if the many conservation projects that are planned and underway are to be based on a sound and reliable base of understanding. Thus, the ten projects proposed here are not directly conservation-orientated. Rather, they are aimed at elucidating aspects and issues that are needed for a more complete understanding of these remarkable birds. In particular, a plea is made for high quality natural history and for cultural sensitivity and awareness.

Introduction

Although it has been almost 480 years since the first European encounter with a megapode (see Frith, 1959), a large proportion of the scientific study of this family has occurred within the last few decades. The coverage of this recent research has been usefully focussed by two recent publications: the monograph on the family (Jones et al., 1995); and the Megapode Action Plan 1995 - 1999 (Dekker & McGowan, 1995). These have encouraged considerable amounts of new work and have been especially valuable in providing a basis for allocating priorities, especially in the light of the urgent conservation needs of many species (Dekker, this volume a).

In the proceedings of the First International Megapode Symposium (Dekker & Jones, 1992), we presented a bibliography of the Megapodiidae, complete from the very earliest publications to 1991. The sheer size of this list surprised many, including those of us working within the field. Here was a family of birds that has inspired and fascinated workers for centuries.

The present volume includes an up-date of the bibliography, this time covering less than a decade (although there are a small number of publications which were missed in the earlier compilation): 1992 to 1998. Clearly, the work is continuing with increased vigour (see Dekker, this volume b).

But much remains to be done. These birds are remarkable in almost every aspect of their physiology, ecology, behaviour and relations with humans and will provide many avenues for fruitful study. Moreover, such studies will also provide a sound scientific basis for essential conservation work.

Conservation-orientated studies are of critical importance; most of the megapode species remain seriously threatened, many increasingly so (Dekker, this volume a). This situation should not, however, lead to a polarity between so-called 'science' research versus 'conservation' research. The timely advent of the field now known as 'conservation biology' has hopefully put this dichotomy to rest (Caughley & Gunn, 1996). Conservation actions fail or succeed on the quality of the science on which they are based. Obviously, there would seem to be little point in conducting, for example, mate removal experiments on an endangered species. Nonetheless, it may be that the mating system is the key to understanding why the species is in decline. In such a delicate situation, reliable science is not just interesting, it is essential as a basis for sound conservation management (Caughley & Gunn, 1996).

Much earlier this century, one of the most influential figures in practical wildlife management observed: "So far, we have the scientist, but not his science, employed as an instrument of ... conservation" (Leopold, 1933). I would endorse and slightly expand this remark as we face the daunting and emotional issues that confront megapode conservation into the new millennium: let our science serve our conservation goals.

This also implicitly acknowledges something we are often reluctant to face: that conservation is a human goal, closely associated with cultural influences (Hargrove, 1989). Although such sociological, anthropological or even philosophical considerations may seem far removed from the real-world of conservation, these are issues of profound importance to megapode biologists (see Pearl, 1989). Megapode survival and extinction has been, and remains, closely tied to human societies (Steadman, this volume). The fate of many species will depend on people in communities in remote locations quite unlike our own. The challenge will be knowing how best to translate our science, our conservation goals, and our practice into forms accessible, intelligible and valuable to societies with often markedly different histories and priorities.

Here I identify ten research projects for which the megapodes would appear to be highly suitable subjects of study. These projects are positioned within four major areas: (a) Ecophysiology and Adaptations; (b) Evolution and Behaviour; (c) Population Studies; and (d) Management. I hope these will provide a spring board for additional ideas from others. In the light of the comments above, I do not include issues directly associated with conservation; Dekker (this volume a) has covered that area thoroughly. In some cases, the projects are based on existing studies; in others, the questions arise from research in other fields but may be worth pursuing among the megapodes. Obviously, this selection is personal, biased and idiosyncratic. But I also hope it is particularly interesting. In addition, I devote more time to some issues than others. This should not be taken as any indication of importance or priority.

(a) Ecophysiology and Adaptations

(1) Mechanisms and manipulation of heat production in mounds

We appear to know quite a lot about incubation mounds (see Jones et al., 1995), although, as with almost all aspects of megapode biology, the details come from a very few well studied species (e.g. Seymour, 1985; Jones, 1988a). One aspect of mound construction of interest relates to the remarkable variety of mound types that have been recognised within a single species (e.g. Coates, 1985; Dekker, 1989, 1992). The interest here is not one of inter-year variation or even individual differences but rather in gross differences in size, location and even nature of construction. Sankaran (1995) and Sankaran & Sivakumar (this volume) have described such mound types in Nicobar megapodes *Megapodius nicobariensis* Blyth, 1846, and has asked whether these constructions may utilize different sources or particular mixtures of heat (see also Dekker, 1989).

Although Seymour and co-workers (e.g. Seymour, 1985; Seymour & Bradford, 1992) have added enormously to our understanding of heat production, maintenance and the influences of mound construction and size for one species (the Australian brush-turkey *Alectura lathami* J.E. Gray, 1831), there is much we do not yet know about these processes in other species, or even the same species in different environments (for instance, Australian brush-turkeys in dry inland forests (Blakers et al., 1984). Of particular interest would be mound builders living in very warm and moist environments. Furthermore, we are still extremely ignorant of these processes (and their influences on embryos) for almost all of the burrow nesters.

The careful and sophisticated temperature manipulation of the malleefowl *Leipoa ocellata* Gould, 1840, remains one of Frith's major discoveries (Frith, 1956, 1957) and it is certainly one of the most enduring impressions of megapodes in general (cf. Jones, 1989). However, to what extent is temperature manipulation a feature of other species; e.g., Jones (1988a) suspected that Australian brush-turkeys did not directly alter mound temperatures?

(2) Embryonic and pre-emergence adaptations

The processes, both evolutionary and proximate, that enable a megapode embryo to survive, grow, hatch and emerge from the depths of a mound or burrow are among the most astonishing adaptations exhibited by this remarkable family. While excellent work has been completed (e.g. Vleck et al., 1984; Seymour et al., 1986, 1987; Booth, 1988), these again have been limited to a couple of species. Much more information is required on egg shell structure and changes over the incubation period (as it relates to gas exchange), gas exchange in burrow nesters (where the gaseous environment is not controlled by the birds), mechanisms of hatching, and the numerous physiological problems associated with the initiation of breathing.

(b) Evolution and Behaviour

(3) Description and function of vocalizations

Göth's contribution to this proceedings (Göth et al., this volume) is the first detailed publication on vocalizations for any megapode species. While obviously invaluable, its lonely status highlights a serious deficiency in our coverage of megapode behaviour. This is of particular importance because of the central role vocal behaviour plays in the social and sexual interactions among perhaps a majority of bird species. Moreover, seemingly complex vocalizations and possibly even 'song' (see Göth et al., this volume), are highly unusual among non-passerines. A crucial first step will be the careful recording and description of the vocal repertoire of each species.

The *Megapodius* Gaimard, 1823, and *Talegalla* Lesson, 1828, species are all quite vocal, calling at all times of the day and night (Lincoln, 1974; Coates, 1985; Jones et al., 1995). The function of these calls is far from obvious and may differ among species. Similarly, *Macrocephalon* S. Müller, 1846, *Aepypodius* Oustalet, 1880, and *Leipoa* Gould, 1840, also produce numerous calls, and again, our understanding of these is far from complete (Jones et al., 1995). In the latter species, postures may also be involved in signalling (Böhner & Immelmann, 1987).

While 'noisy' megapodes pose a particular set of questions, the seemingly 'quiet' species pose yet another. The Australian brush-turkey is remarkable in being by far the most non-vocal megapode, its repertoire being mainly low-level clucks and grunts. It does, however, produce a deep 'boom' via its air filled neck wattle. Again, the function is not well understood. Is this 'boom' similar to that of the malleefowl? Possibly, this species' communication forms are both vocal and visual (see below).

The role and importance of duetting among the megapodes is now slowly being addressed (Göth et al., this volume); Göth et al. indicate that many species are known to duet but also shows how little is known reliably. Again, careful observations and high quality recordings are essential. Duetting will be a crucial element in advancing our understanding of megapode mating systems, clearly much more complex than originally thought (e.g., see Sankaran & Sivakumar, this volume; Birks, 1997; cf. Jones, 1992).

(4) Structure and function of phenotypic features such as wattles, combs, cephalon, and phalli.

Megapodes possess a number of rather unusual structural features. For example, the maleo's *Macrocephalon maleo* S. Müller, 1846, astonishing cephalon or casque, demands further investigation, particularly experimentation and field observations (Starck, 1988; see summary in Jones et al., 1995).

There are also a variety of fleshy parts. The brush-turkeys of the genera *Alectura* Latham, 1824, and *Aepypodius* possess a bizarre array of head and neck appendages (see plates in Jones et al., 1995). Some of these are employed for vocal display, being inflated with air and used in various vocalizations. The most spectacular is the enormous expansion of the Australian brush-turkey's wattle for the purpose of the boom, although the malleefowl appears to produce its boom similarly. How these structures are actually used - the physiological aspects - would be most interesting.

However, these head and neck appendages are also used in visual communication. The colours are often bright - vivid yellow and scarlet - and the structures may be enhanced by expansion or being filled with air (e.g. see Kloska, 1986). The function of these appendages is very poorly known (see (5) below).

Another structure of great interest is the male phallus. Considerable interest has been raised recently by the apparent correlation between large and dramatic 'sperm delivery' devices, especially among species with clearly non-monogamous mating system (e.g., see Frey, 1995). My initial investigations suggest that this may be relevant among the megapodes. Earlier (Jones, 1992), I speculated that megapodes tend to be either strictly monogamous or not at all. This is admittedly a simplistic polarity. Nonetheless, most of our data to date do suggest that the majority of species are at least socially monogamous most of the time (Jones et al., 1995) (The occasional breeding trio among malleefowl, for example, may be regarded as obvious opportunism and unlikely to be anything but a rarity (see Weathers et al., 1990)). Conversely, just a few species, again the brush-turkeys, exhibit no pair bonding as such, with males mating with multiple females and extra-pair copulations being relatively common (Birks, 1997).

If this dichotomy of monogamy/non-monogamy is 'deep-seated' in evolutionary terms (as opposed to being highly plastic), non-monogamous males may possess a sperm delivery structure suited to efficient internal insemination. This hypothesis would predict that the non-monogamous brush-turkeys should possess an intromittent organ, while most of the others should not.

Our only data show that, in *Alectura*, males do indeed possess a strange double-headed phallus, so conspicuous that it allows sexing within days of hatching (unpublished data) while the malleefowl, the only other species inspected to date, does not. Obviously we need more data from all genera, especially *Aepypodius* and the little known *Talegalla*.

(5) Sexual selection and mate choice, including the role of parasites and colour signalling.

The process and phenomenon of sexual selection is definitely one of the most influential and active studies on modern evolutionary research at present (Ryan, 1997). Species which have marked sexual dimorphism, or special features such as elaborate behaviours or structures are particularly interesting because of the questions that arise as to their origin and function. For example, are the odd facial structures of the brush-turkeys used by females to select mates, by males to enhance this choice, or do they simply form some much more prosaic function, like noise production?

There are two specific areas that may be of particular interest: parasites and colour.

Hamilton & Zuk (1982) promoted the very provocative idea that parasites may be involved in the evolution of some of the prominent colours we see today in birds. Simplistically put, they proposed that males could advertise that they were parasite-free by evolving colours or structures that would be clearly and obviously affected by parasites if they were present. For example, red pigments are physiologically expensive to maintain and are easily dulled by parasites (e.g. Zuk et al., 1990). Similarly, bright feathers will soon become shabby if loaded with chewing lice (e.g. Borgia, 1986), and bare skin becomes blotchy and pale if the bird is infested with ticks and mites. By exposing or expanding such areas or colours, parasite-free males would be able to advertise their superior status, while parasite-affected males would not be able to hide their condition.

Features which could be involved in this newly described mode of sexual selection are clearly evident in a number of genera among the megapodes: the brush-turkeys, of course, but also the talegallas. Moreover and interestingly, at least eight of the *Megapodius* species also have some bare, red sections of the face. This is definitely an area of considerable promise.

A new and illuminating area of research related to this discussion of colour has recently been advanced by Endler (1992). This concerns the influence of light environments on the evolution of colours. He has demonstrated that the frequencies of ambient light used in reflecting the colours of the plumage are very different in different places. For example, open grassland receives all the sunlight and sky light whereas there is varying filtering effects of this ‘whole’ light as it travels through and is reflected from and by the canopy and under layers of forests or rainforest. By the time this light reaches the forest floor, the remaining frequencies will give a distinctive nature to the available light environment. These theories allow predictions of how birds might use their colours, having evolved to take advantage of the light that exists where they live.

For example, Australian brush-turkeys are basically red, yellow and black, all colours that do not reflect well in the shade. I have shown (Jones, 1988b) that mounds are selected by males to be in particularly shaded places, for reasons of moisture conservation and leaf supply. That is, it seemed clear that males were primarily concerned with the functioning of their mounds. But, as males also do most of their performance for females on this decidedly dark mound, this appeared to counter Endler's argument. However, Endler recently predicted (pers. comm.) that the reds and yellows of the brush-turkey's head and neck would be most conspicuous in shafts of unfiltered light. We have since found that a large number of mounds do receive beams of light at some stage during the morning, allowing the previously drab owners to explode into colour.

However, what about the rest of the time, when the male brush-turkeys really are stuck in the dark? Again, Endler (pers. comm.) pointed out that birds in general see far into the ultraviolet; maybe the shade is not such a problem if the colours reflect in these wavelengths. Sure enough, colleagues at the University of Queensland have recently confirmed that the yellow neck wattle radiates powerfully in ultraviolet light (I. Owens, pers. comm.). These are question especially important for species with courtship displays.

(6) Mechanisms, extent and importance of sperm storage and sperm competition.

Sperm competition is an extremely sexy issue at present (Birkhead & Parker, 1997). The role of the female in most mating systems has traditionally been regarded as one of a passive partner, meekly accepting the dictates of the dynamic, all-powerful male (Davies, 1991). This idea has been convincingly routed by many studies of female behaviour (Bateson, 1983) which have shown astonishingly sophisticated mate choice by females in many species (including megapodes; see Birks, 1996, 1999).

The discovery that females are able to store sperm from one or numerous males, and even possibly influence which males fertilize which offspring, has been one of the most surprising and influential areas in contemporary evolutionary biology (Birkhead & Möller, 1992). Its potential importance to megapodes is obvious and raises many questions. Females of every species of bird so far examined appear to possess small tubules within her lower reproductive tract which store the sperm immediately after mating, and this is released at a later time (Birkhead & Möller, 1992). These issues are especially important for those megapodes where there is no pair bond and where females may be impregnated by numerous males. The brush-turkeys, again, are obvious candidates for further studies in this area.

One aspect we hope to address ourselves concerns quantifying the amount of sperm actually involved in the competition for fertilization. Although the ovum is surrounded by a swarm of millions of sperm, only one is able to penetrate the membrane covering the ovum. At the instant of penetration by the first "lucky" spermatozoan, the membrane solidifies, preventing any further penetration. But in the process of the formation of this perivettiline layer, vast numbers of sperm become trapped (Birkhead et al., 1994). If we can extract the DNA from these sperm we will be able to establish the precise probabilities of males involved, a technique potentially applicable to other birds.

The sophisticated molecular techniques required for these studies should be applied to the apparently 'monogamous' megapode species as well. Perhaps the greatest discovery to emerge from the explosion in DNA-based parentage studies is that the term 'monogamy' is essentially a description of social relationship (e.g. Lack, 1968); the vast majority of bird species, which breed in seemingly strict pairs, are now known to commonly engage in extra-pair copulations (see Westneat & Sherman, 1993). This recent history suggests extreme caution as we attempt to describe megapode mating systems from observations alone!

(c) Population Studies

(7) General population ecology, especially recruitment, survival and dispersal, and influences of predators.

Let us not get carried away on too much esoteric minutiae, however inherently interesting. We can hardly rest on our laurels when so many of the most basic aspects of megapode biology and ecology remain largely unknown. As will be obvious to all by now, the overwhelming majority of studies have been based on a very few species. And the really alarming reality is that, even for the common species, we have only a rudimentary understanding of most crucial population level features.

The list of questions would be virtually endless but some important ones to start with relate to chicks and hatchlings, perhaps the most important areas of almost complete ignorance (Jones, in press). Wong (see this volume) is, to date, the only worker to focus on young birds; hopefully others will become involved in this intriguing area. In particular, Wong (unpublished data) has shown that, contrary to expectations, there is no evidence of imprinting in Australian brush-turkeys, a result very likely to apply to all megapodes. This finding raises many questions, including aspects associated with evolution of behaviours: have megapodes lost this seemingly universal galliform trait, and if so, how did it happen?

Some other questions are:
Is there sex-biased dispersal?
What is the really dangerous time for survival and why?
How important is starvation or lack of free water to hatchlings?
Are there general predator issues to all megapodes?
When do chicks move from anti-social to pro-social behaviour?

(8) Genetic structure at the population level, especially in relation to species boundaries.

The production of Jones et al. (1995) provided the first generally accepted list of species and subspecies for the Megapodiidae (Roselaar, 1994), an enormous tribute to our colleague Cees Roselaar and possibly enabling a much greater focus on distributions and processes of speciation. But the maps and statements in Jones et al. (1995) also raise many questions about the exchange between populations and the reality of species boundaries. There are many species-boundary 'hot-spots' that would be very interesting to visit (some are listed in the book) especially in the vastness of the New Guinea island, where sympatry, possible hybridization and uncertain distributions are evident.

(d) Management

(9) Useful management models.

Foremost among the many reasons for the largest ever gathering of megapode workers was the undeniable reality that these astonishing birds are in serious trouble almost everywhere. Their survival will require a very major effort by large numbers of people. But the bottom-line is that people will have to do things: birds will need to be counted and observed; eggs collected and possibly translocated; habitats manipulated. That is, management is required. However, this management must be based on the best knowledge, must be useable and effective, and, above all, must be *sustainable* in nature. This is no longer simply a 'buzz-word' of the academy. Sustainable management will be multifaceted and multidisciplinary, involving people from afar and locally (Pearl, 1989; Norton, 1989). This, in the end, may be our greatest area of ignorance and therefore, will require our greatest willingness to learn.

(10) Cultural engagement

The active participation and engagement with the World Pheasant Association in the Third International Megapode Symposium had many positive outcomes. But perhaps, one of the less obvious may be an appreciation by others of the careful, long-term, patient working with local people. It goes without saying that conservation in the developing world must be acutely culturally sensitive, as well as pragmatically based. With so many of megapode species deeply imbedded within the cultural setting of a variety of groups (see Göth et al., this volume, Sankaran & Sivakumar, this volume, Baker, this volume), attention to cultural aspects will be as important as technical and intellectual skills (Norton, 1989).

A plea

Finally, may I make a plea for attention to one additional area: all this work will require good, old-fashioned natural history skills. We have, I hope, learned from the relentless reductionism of our recent past: a deep understanding of the animals that inspire us requires a variety of approaches, none more important than the ability to remain curious.

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