

## MODERN MEGAPODE RESEARCH A POST-FRITH REVIEW

DARRYL N. JONES

Division of Australian Environmental Studies, Griffith University, Nathan, Old 4111

Received 30 March, 1989

Modern studies on the megapodes commenced with H. J. Frith's studies on the Malleefowl *Leipoa ocellata* during the 1950's. Since this time much debate has centred on the evolution of the family, especially on taxonomic relationships and routes of dispersion. More recently, major advances in the understanding of megapode incubation have been made, especially the functioning of mounds, and the associated adaptations of eggs and chicks. Detailed studies of sexual interactions have revealed numerous types of mating systems within the group, leading to speculations as to their evolution. Many species are currently threatened, and many areas of ecology and behaviour remain to be studied.

### INTRODUCTION

The megapodes (Megapodiidae), also known collectively as the 'mound-builders', are among the most fascinating yet least studied families of birds. Ever since their discovery during Magellan's 1519–1522 expedition (Frith 1959a), the birds have fascinated and perplexed travellers, naturalists and scientists alike. It has been their use of environmental sources of heat for the incubation of eggs that has attracted most attention. Moreover, no other birds provide so little parental care as the megapodes: eggs and chicks are effectively abandoned at the incubation sites. Initially regarded as anatomically archaic (Clark 1964a), this apparent reptilian trait was taken as further evidence of the primitive stage of evolutionary development of the family (Frith 1956a; Clark 1964b).

Although there are important exceptions (Barrett and Crandal 1931; Fleay 1937; Coles 1937), the foundations of modern megapode research were laid by H. J. Frith. His decade or so of work on the Malleefowl *Leipoa ocellata* (Frith 1956b, 1957, 1959b, 1962a, 1962b) drew worldwide attention and provided the basis for a scientific understanding of the family as a whole. Frith also provided a detailed coverage of the

scattered and often obscure literature in two comprehensive reviews of incubation habits within the family (Frith 1956a, 1959a), and also speculated on their evolutionary origins. Clark (1964a) extended this information to examine critically the hypothesis of a direct reptilian ancestry; he saw the methods of incubation as remarkable secondary adaptations, suggestive of evolutionary specialization.

Clark (1964b) and more recently Diamond (1983) have provided concise summaries of the research conducted during the 1960's and 1970's. During the past decade, however, many major advances in the understanding of the physiology, ecology and behaviour of numerous megapodes have been made. It is the aim of this review to provide a brief overview of the most pertinent of these discoveries. This cannot pretend to be exhaustive; rather, the intention is to update scientific views of these birds, to stimulate interest, and overall, to demonstrate the need, potential, and value of further study.

### TAXONOMY AND MORPHOLOGY

Although one species, the Australian Brush-Turkey *Alectura lathami*, was initially classified as a vulture (Gould 1865), there has been little doubt

that megapodes are closely allied to other species within the Order Galliformes. Within this Order the megapodes are the most distinctive family (Olson 1980), and, with the New World Family, the Craeidae (chachalacas etc.), have been classed as the most primitive.

Apparent affinities between the megapodes and cracids have been greatly strengthened by the recent taxonomy of Sibley, Ahlquist and Monroe (1988). In a revolutionary step these authors have separated these two groups from the other Galliformes into a separate Order (the Craciformes). The veracity of this classification will necessitate testing from other sources of evidence.

All megapodes show great structural similarity and are distinctly monophyletic in origin (Clark 1964a). The Malco *Macrocephalon maleo* shows the greatest skeletal divergence within the family,

possessing a large helmet-like casque on the back of the skull. Stark (1988) has shown this to be of pneumatized bone, not horn as often reported. The structure and attachment of the casque to the skull is analogous to that found in some woodpeckers and suggests a similar shock-absorbing mechanism. This may be related to their habit of hammering hard-shelled nuts observed during feeding (R. Dekker, pers. comm.).

The extant Megapodiidae consists of six genera, currently comprising 19 species (Table 1). The family contains three monotypic genera: *Alectura*, *Leipoa* and *Macrocephalon*. *Alectura* is considered to be closely related to *Talegalla* and *Aepyodius*, a group known as the brush-turkeys, each having a bare beak and face which may be brightly coloured (Coates 1985; Beehler, Pratt and Zimmerman 1986). *Alectura* and the two *Aepyodius* species also possess inflatable neck

TABLE 1

The Megapodes: names, distributions and status.

Genus	Species	Common name <sup>1</sup>	General distribution <sup>2</sup>	Conservation status <sup>3</sup>
<i>Leipoa</i>	<i>ocellata</i>	Mallecfowl	Australia, inland	2
<i>Alectura</i>	<i>lathami</i>	Australian Brush-turkey	E Australia	4
<i>Talegalla</i>	<i>cuvieri</i>	Red-billed Brush-turkey	W Irian	4
	<i>fuscrostris</i>	Black-billed Brush-turkey	S New Guinea	4
<i>Aepyodius</i>	<i>johienstis</i>	Brown-billed Brush-turkey	N New Guinea	4
	<i>arjakanus</i>	Wattled Brush-turkey	Upland New Guinea	3
	<i>bruijnii</i>	Bruijn's Brush-turkey	Waigeo Island	1
<i>Macrocephalon</i>	<i>maleo</i>	Malco	Sulawesi	2
<i>Megapodius</i>	<i>nicobariensis</i>	Nicobar Scrubfowl	Nicobar Island	1
	<i>cumingii</i>	Philippine Scrubfowl	Philippines to Sulawesi	4
	<i>bernsteinii</i>	Sula Scrubfowl	Banggai and Sula	2
	<i>reinwardi</i>	Orange-footed Scrubfowl	Kangean Island to N Australia	4
	<i>freycinet</i>	Dusky Scrubfowl	N Moluccas	4
	<i>affinis</i>	New Guinea Scrubfowl	N New Guinea, offshore islands	4
	<i>eremita</i>	Melanesian Scrubfowl	Karkar to Solomon Islands	3
	<i>layardi</i>	Vanuatu Scrubfowl	Vanuatu	2
	<i>pritchardii</i>	Polynesian Scrubfowl	Mariana and Palua Islands	2
	<i>laperouse</i>	Micronesian Scrubfowl	Nivalo'ou Island, Tonga	2
	<i>wallacei</i>	Moluccan Scrubfowl	Moluccan Islands	2

<sup>1</sup>After Dekker 1988a; White and Bruce 1988.

<sup>2</sup>For detailed distributions see Beehler *et al.* 1986; Blakers *et al.* 1984; Coates 1985; Dekker 1989; Ripley 1960; White and Bruce 1986.

<sup>3</sup>Conservation status: 1: Seriously endangered; 2: Threatened, conservation measures required; 3: Secure but uncommon or some populations threatened; 4: Widespread and abundant (see Coates 1985; Megapode Specialist Group 1988).

saes or wattles (Jones 1987; Kloska and Nicolai 1988).

The genus *Megapodius*, or scrubfowl, are the smallest megapodes. Geographic variation is considerable but most are chicken-sized birds with short tails and a short pointed nuchal crest (Beehler *et al.* 1986).

Relationships among the extant megapodes are far from certain. Clark (1964a) proposed a two branch system: one side diverging to the brush-turkeys with *Leipoa* branching off before *Alectura*; the other with *Macrocephalon* as an early branch, with the scrubfowl being the most recent species. This provisional phylogeny is likely to be challenged by a number of current studies investigating comparative anatomy and embryology, morphogenetic development, the microstructure of feathers, and egg characteristics.

#### ORIGINS AND BIOGEOGRAPHY

One of the implications of the revised relationships between the megapodes and other families (Sibley *et al.* 1988) is that of reviving support for a Gondwanic origin for the family. This view, advanced mainly by Cracraft (1973), hypothesized a trans-Antarctic dispersal history of ancestral megapodes into Australia. These birds, and a suggested proto-cracid group, were derived from ancestral galliforms inhabiting Gondwanaland in the Cretaceous (Cracraft 1973). This idea was criticized by Olson (1980), who favoured a North American centre for the cracids, arguing that this group would not have been in South America at a time appropriate for dispersal across Antarctica. Olson (1985) maintained that a northern movement into Australia was the most likely route, citing in support the recent discovery of a small late Eocene megapode in France. Certainly a very large species (*Progura gallinacae*) occurred in south-eastern Australia during the Pleistocene, and differed only in size from modern megapodes (Rich and van Tets 1985). Elsewhere Balouet and Olson (1989) have described an extinct species, *Megapodius molistructor*, from New Caledonia; their palaeontological and archeological studies indicate a much wider distribution of megapodes in the past, especially in the south-east Pacific.

One of the major problems with the idea of a southern movement of megapodes into Australia is their current absence from the Indo-Himalayan region (Olson 1980). Conversely, the distribution

of the Phasianidae (pheasants and quails), the largest family in the Galliformes, extends westward throughout this region with virtually no overlap with megapodes (Olson 1980). Olson (1980) attributed this distribution to some form of competitive exclusion, noting that despite the megapodes superior abilities to disperse over water (Ripley 1960), phasianids appear to have displaced megapodes wherever they meet, thus preventing their spread northwards. This picture has been complicated somewhat by relatively recent translocations of Junglefowl *Gallus* spp. and scrubfowl onto many Indo-Pacific Islands (Ripley 1960).

The almost perfectly complementary distributions of the megapodes and the phasianids is striking. Dekker (1989), however, doubted whether ecological competition offers sufficient explanation. Rather, he argued that the occurrence of certain carnivores was a key factor not only of the distribution of the megapodes but also in the types of incubation (mound versus burrow) developed in the eastern distributed species.

Currently megapodes are very widely distributed throughout the south-east Asian and Melanesian island chain (Fig. 1), from the Nicobar Islands to Niuafou, near Tonga, and throughout an area 22 degrees north and south of the equator (Blakers, Davies and Reilly 1984; Rinke 1986). Within this vast area, the species have spread onto many extremely remote and small islands as well as occurring on most of the larger land masses. Olson (1980) and Dekker (1989) provide the most accurate maps of megapode distributions, correcting earlier inclusions of Sumatra, Java and all but the northern extremities of Borneo (Frith 1959a; Clark 1964a). The greatly disjunct occurrence of *Megapodius* on the Nicobar Islands is problematic. It may be a relict population surviving from an early period of expansion, the consequence of recent colonization of the Nicobars, perhaps by island hopping along the islets off Sumatra and Java (Olson 1980), or via introductions by humans (Lister 1911). Whatever the agency, *M. nicobariensis* remains very similar to others within the genus (White and Bruce 1986).

#### ADAPTATIONS TO UNDERGROUND INCUBATION

The crucial adaptive achievement of the megapodes, and one that critically influences



Figure 1. The distribution of the Megapodes (after Olsen 1980).

every facet of their biology and behaviour, is their exploitation of external sources of heat for the incubation of eggs. Three main sources of heat are used: solar radiation, geothermal activity, and organic decomposition (Frith 1956a). The eggs may be deposited in beach sand, in burrows, in volcanic areas, under leaves on the rainforest floor, or deep within mounds of decomposing leaf litter (Diamond 1983). In these environments, megapode eggs are exposed to conditions dramatically different to those of normally brooded eggs. Moreover, as incubator temperatures relate not to the body temperature of the brooding bird but to physical, chemical and climatic variables of the site, megapode eggs may be subjected to markedly variable incubation conditions. The intensive studies by Seymour and colleagues have revealed remarkable adaptations to these conditions. This work has been succinctly reviewed by Seymour (1985), and is summarized here, along with more recent studies.

### *The Incubation Mound*

Megapode mounds are among the largest structures made by any non-colonial animal. The considerable effort involved in providing the mound (Jones 1988a) represents the harnessing of the energy of an otherwise small-scale phenomenon (organic decomposition) by concentrating suitable material (moist leaf litter), and sustaining favourable conditions (regular mixing of fresh mound materials) (Seymour 1985). Contrary to earlier opinions, heat results not from fermentation but mainly from the respiration of micro-organisms, principally thermophilic fungi (Seymour, Vleck and Vleck 1986). No location within the mound is anoxic (Seymour and Ackerman 1980).

Temperatures increase with depth into the mound, and although the core of a mound may be 36°C or higher (Seymour and Rahn 1978), the average temperature at the depth of the eggs is

often about 33°C (Frith 1962a; Jones 1988b, 1988c). Temperatures may, however, vary greatly between mounds and over time: five species showed a range of 31–39°C (Seymour and Ackerman 1980) with the greatest within-species variation being associated with burrow-nesting species (Mackinnon 1978; Todd 1983; Dekker 1988b).

Higher incubation temperatures accelerate embryo development but may be deleterious if certain specific limits are exceeded. Maintaining the thermal stability of the mound involves balancing heat production with heat loss (by diffusion through the mound material). Malleefowl have evolved the most sophisticated (and arduous) techniques of mound temperature maintenance, involving continual removal and replacement of a thick insulation layer to expose the inner decomposing core (Frith 1962a). Successful mound maintenance requires both the correct assessments of heat and moisture content, and the appropriate utilization of solar and microbial heat by manipulating mound structure (Frith 1956b, 1957).

Other mound-building species rely solely on microbial respiration for heat production; most of the decomposition occurs not only in the core as in Malleefowl, but either throughout the mound (e.g., Australian Brush-turkey, Jones 1988c) or at specific locations activated by the bird (e.g., Orange-footed Scrubfowl, Crome and Brown 1979).

It is clear that activities such as adding and mixing fresh material, or changing mound shape to either lose or conserve moisture (Baltin 1969), are essential for the maintenance of temperature levels (Seymour *et al.* 1986). Although Frith (1957) demonstrated the ability of male Malleefowl to alter mound temperatures, Seymour (1985) has proposed that physiological characteristics of the mound itself are important in thermal stability. Based on the less complex Brush-turkey mound, Seymour's model shows the heat production and heat loss will tend to stabilize mound temperatures at an equilibrium state. This phenomenon is due to the great thermal inertia of the mound, and the self-stabilizing relationship between loss and production of heat (Seymour 1985). Thus, given a minimum size (0.75 m high and 2 m diameter), and regular additions of fresh moist material, mound temperatures should remain within some small range.

Seymour's mound homeothermy model has recently gained support from observations of Brush-turkeys (Jones 1988c), where four mounds maintained thermal stability long after being abandoned. Even more valuable support was obtained from a Malleefowl mound with an internal temperature of 35°C seven weeks after abandonment (Weathers, Weathers and Seymour 1989). These data indicate a thermal inertia even more pronounced than that of the model, and suggest that normal mound maintenance activities may be associated less with the regulation of a particular temperature and more with perpetuating microbial activity as the force driving mound homeothermy (Jones 1988c).

#### *Adaptations of the egg*

Throughout incubation, the survival of the developing embryo depends on the diffusion of oxygen, carbon dioxide and water vapour through the shell. This gas exchange is regulated by the conductance of pores in the shell, and the difference in gas tension across the shell (Booth and Seymour 1987). In most birds shell conductance leads to a water loss during incubation equivalent to about 1 per cent of the initial egg weight, a process also associated with the formation of the airspace used by the embryo to breath prior to hatching (Seymour 1985).

The often extreme humidity of megapode mounds eliminates the risk of eggs dehydrating but should also restrict gas exchange to the embryo. Despite these apparently unsuitable conditions, gas tensions inside megapode eggs from field mounds were almost identical to other birds eggs (Seymour *et al.* 1986). This outcome, providing optimal gas exchange to the embryo, is related to the remarkably high conductance of the shell — about twice that predicted from normal birds (Seymour and Rahn 1978), and is due to the unusual thinness of the shell. The thickness is only 69 per cent of that predicted from initial egg mass, substantially thinner than other Galliformes (Booth 1988). Pore area, however, is not greater than expected, and pore number and structure are assumed not to alter during incubation (Seymour and Rahn 1978).

Despite the high humidity within the mound, megapode eggs do lose 10–12 per cent of their initial mass during incubation (Seymour, Vleck, Vleck and Booth 1987). What is particularly interesting is that this evaporation rate increases three-fold during the incubation period (Booth

and Seymour 1987), indicating a major change in shell conductance. This results from two factors: water vapour conductance increases with ambient humidity (Seymour *et al.* 1987), and changes in pore structure due to the absorption of shell calcium by the embryo for skeletal ossification (Booth and Seymour 1987). This change in conductance enables the embryo to undertake the necessary gas exchange, while conserving water during the crucial early stages of development (Seymour *et al.* 1987).

#### *Adaptations of the chick*

The environmental conditions associated with underground incubation also impose particular stresses on the chick even prior to hatching. One of the consequences of reduced egg dehydration is that no useful air space is formed (Seymour and Rahn 1978). In other birds, this space is used for the chick's initial pulmonary respiration, well before hatching. Megapode chicks, however, can take their first breath only after the shell is broken and the membrane ruptured. This critical event occurs very rapidly, the thin shell being shattered by the well developed legs (Baltin 1969), as there is no functional egg tooth (Clark 1964b). Breathing begins immediately, and chorioallantioic circulation stops within two minutes (Seymour 1984).

Following hatching the chick faces an exhausting passage through 40–80 cm of soil and organic matter (Frith 1956a; Jones 1988b). This process may take two to 15 hours in Malleefowl (Frith 1959b) and up to two days in Brush-turkeys (Baltin 1969), adding substantially to the energy expenditure associated with incubation (Vleck, Vleck and Seymour 1984). Overall, this energy expenditure is much higher than predicted by the egg sizes and other precocial species (Vleck *et al.* 1984). The adaptive significance of this is seen in the chick's extreme precocity. Though weighing only 65 percent of its initial egg mass (Seymour *et al.* 1987), the chick has well developed primary feathers and a thick layer of pennaceous feathers, in contrast to the usual down of other Galliformes (Clark 1960). In this state it can run immediately, fly within the day (Baltin 1969) and, more critically, thermoregulate effectively over a broad range of temperatures (Booth 1984, 1985). Malleefowl chicks, in particular, are tolerant of temperatures between 3° and 46°C (Booth 1984).

#### *Extreme precocity of hatchlings*

Megapode chicks are the most precocial of all birds (Nice 1962) and they certainly need to be.

Receiving no direct parental care or assistance from the time eggs are laid, young megapodes must feed, avoid predation, and survive climatic vagaries entirely alone from the moment of hatching. The advanced stage of development at which they emerge from the egg correlates with the energetic capital invested in the eggs, and with the long period of incubation. Megapode eggs are about 3.5 times larger than expected for Galliformes (Seymour and Rahn 1978) and are energy rich (Vleck *et al.* 1984), meeting the high energy demands through unusually large yolks (50–70 per cent of egg content, Seymour 1985). The eggs are incubated for 49 (Brush-turkeys) to 62 (Malleefowl) days (Vleck *et al.* 1984), particularly long periods for birds, but the growth rates of the chicks is very similar to other Galliformes (Baltin 1969). Thus, although megapode chicks are two to 15 times heavier at hatching than expected from other Galliformes (Seymour and Ackerman 1980), this is due mainly to several weeks of prehatching development associated with the longer incubation period (Seymour 1985).

### MATING SYSTEMS

The reproductive behaviour of most megapode species strongly suggests that most are distinctly monogamous (Crome and Brown 1979; Immelmann and Bohner 1984; Bohner and Immelmann 1987). In general, two contrasting types of social organization are evident: (1) pair-bonds are obvious and permanent, mated birds being virtually inseparable; and (2) males and females form close pair bonds but spend considerable periods apart. These social types are typified by various burrow-nesting species (Ripley 1960; Lincoln 1974; Crome and Brown 1979), and mound-building Malleefowl (Frith 1962a), respectively. Nonetheless, most species exhibit features often associated with strong pair-bonding, such as duetting, exhibiting highly synchronized behaviours, and monomorphism. For example, Immelmann and Bohner's (1984) description of sexual behaviour in Malleefowl pairs outside the breeding season provides strong support for perennial monogamy in that species. Furthermore, these authors suggested that monogamy may be inevitable among all mound-building species. They equated the provision of the incubation site, in Malleefowl a task principally undertaken by the male, with male parental care. Extensive paternal care, rare in birds, is only expected where males can be sure that their parental care is benefiting their own progeny (Trivers 1972). Thus, mound-building

was seen as circumstantial evidence of paternal certainty, and confirmation of monogamy (Maynard Smith 1984).

These ideas suggested that monogamy may be universal within the family, although the distinctive dimorphism among some brush-turkey species cautioned against this generalization. Baltin (1969) found no evidence to suspect anything other than monogamy in captive Australian Brush-turkeys. It was therefore of great interest to find that wild Australian Brush-turkeys exhibited no evidence of pair-bonding (Jones 1987, 1988c). Rather, the sexes live independent lives, meeting only to copulate and lay eggs, with males remaining near their mounds (Jones 1989). Mounds are vigorously defended; many males abandon their mounds due to expulsion by other males (Jones 1988c).

Females may lay 18–24 eggs during a season (Frith 1956a), at intervals of 2–5 days (Vleck *et al.* 1984). In order to have her eggs incubated, a female must visit a mound (Jones 1988c). This enables a mound-tending male to copulate, often repeatedly, with each female visiting his mound (Jones 1989). Females are, however, free to choose among mound-tending males, the males being tied to the location by the imperative of site defence. Both sexes mate promiscuously; males copulate with all females visiting mounds, while females visited numerous males (Jones 1987, *in press*). These findings suggest that, in Australian Brush-turkeys at least, incubation mounds are not exclusively a method by which males incubate eggs, but are also a resource males control to improve their breeding success. Some males construct two mounds, potentially increasing their chances of copulating with more females (Jones 1987).

Compared to the closely co-ordinated behaviours of paired Malleefowl (Immelmann and Bohner 1984), associations between individual male and female Australian Brush-turkeys were cursory and aggressive. Males typically pecked laying females savagely throughout egg laying (Jones 1990) and chased them from the mound immediately afterwards. Very similar behaviours have been recently reported among captive Wattled Brush-turkeys (Kloska and Nicolai 1988). This species also bears inflatable neck wattles and may have a similar mating system.

Despite these contrasting male-female interactions, Malleefowl and Australian Brush-turkeys also share many important features: males are

responsible for the selection of the mound site, and for most or all of its construction, maintenance and defence (Frith 1962a; Jones 1988a, 1988c). Thus, preoccupied with the site, males cannot guard females who wander far from the mound (Frith 1959b). Inevitably this spacial independence of the sexes must reduce paternal certainty, a risk high among Brush-turkeys (Jones 1990), but deemed unlikely among the sparsely distributed Malleefowl (Frith 1959b).

It is axiomatic that males should act to protect paternity and prevent cuckoldry (Maynard Smith 1984). Although remaining to be confirmed, it is likely that Brush-turkey mounds do contain chicks sired by more than one male, in apparent contradiction of current theory (Trivers 1972). This conundrum diminishes, however, if mounds are viewed primarily as a method by which males attract females; the addition of another male's eggs to the mound does not reduce the quality of incubation to his own eggs (within limits) (Vleck *et al.* 1984). Moreover, by enforcing copulation of all laying females, a male ensures that his sperm has pre-eminence as ovulation usually follows soon after fertilization (Sturkie 1976).

Recent observations indicate that opportunities for extra-pair copulations may occur even among Malleefowl. Radiotelemetry by Booth (1987) has shown that both sexes move much farther from the mound than previously expected (Frith 1959b) indicating that other mounds could easily be visited by females. Furthermore, the first verified instance of polygamy in Malleefowl has now been reported (Weathers *et al.* 1989). In this case, one male maintained simultaneous bonds with females at two different mounds.

In contrast, the behaviours of scrubfowl and the Maleo indicate that extra-pair copulations are unlikely in these species. Paired birds remain close together, probably permanently. This continual proximity of paired birds may be interpreted as a technique by which males prevent their mates from contacting other males, thus ensuring their paternity. This 'female-defence monogamy' (Jones 1987; Kloska and Nicolai 1988) is possible only for species in which incubation sites are not defended. A common feature of these species is the communal use of incubation sites, such as geothermal egg-grounds or beaches (Broome, Bishop and Anderson 1984; Mackinnon 1978). Surprisingly, mounds may also be shared by numerous pairs (Crome and Brown 1979).

Little of the behaviour of the *Talegalla* species can be stated with confidence. Although regarded as being very similar to *Acpypodius* (Frith 1956a; Ripley 1960), the lack of sexual dimorphism, the use of loud 'advertisement' calls and duetting (Coates 1985; Beehler *et al.* 1986) indicate affinities with scrubfowl species (Kloska and Nicolai 1988), and suggest a similar form of monogamy.

### CONSERVATION STATUS

Megapodes as a group are seriously threatened. Nine of the 19 species require conservation measures or give reason for concern (Table 1). Probably the most vulnerable species is the Nicobar Scrubfowl, of which less than 400 individuals may now survive. The main causes of population decline are over-exploitation of eggs and adults, and habitat destruction.

The physically large and often easily located incubation sites used by megapodes predisposes both eggs and adults to predation by both humans and other species. Many species suffer great egg losses to varanid monitors (Lincoln 1974; Dow 1980; Mackinnon 1981), while foxes *Vulpes vulpes* have been serious predators of Malleefowl eggs in some populations (Frith 1959b). Generally, however, the long period over which eggs are laid acts against the loss of complete clutches, except in the case of human depredations. Although some harvesting of eggs has probably occurred for centuries, over-use may have been prevented through traditional restrictions (Bishop 1980; Kimber 1985). Declining regard for such laws combined with expanding human settlement now threaten numerous megapode populations (Mackinnon 1981; Broome *et al.* 1984).

Although some populations of these endangered species now exist in reserves (Mackinnon 1981; Broome *et al.* 1984), the specific environmental requirements for breeding also pose special problems. For instance, species using geothermal egg-grounds or beaches, visit these sites only briefly to lay before returning to adjacent forest to feed, and may disperse much greater distances after the breeding season (Frith 1956a; Mackinnon 1978). Therefore, the protection of the egg-grounds may be of little value if surrounding forests are cleared or severely altered (Broome *et al.* 1984).

It is sadly ironic that the best known megapode, the Malleefowl, is seriously threatened, primarily from habitat destruction or modification, and excessive chick mortality

(Brickhill 1987a). The range of the species has diminished (Blakers *et al.* 1984; Brickhill 1984), especially in the central desert regions (Kimber 1985), while most populations have contracted into numerous tiny isolated refuges (Brickhill 1985). In uncleared areas population densities have also declined where sheep grazing occurs (Frith 1962b), but even in ungrazed habitats numbers appear to be falling (Brickhill 1985). Although recent studies found no evidence of declining clutch size (Brickhill 1987b; Booth 1987), Brickhill (1987b) suspected that infertility may be increasing. Brickhill (1987b) also suggested that the fragmentation of the Malleefowl's range into small pockets poses a serious threat to its long-term survival. Pairs probably require large home-ranges, especially in locations with (or during periods of) low food availability (Booth 1987a) and this may severely limit the number of breeding birds able to be supported within a small area. As younger birds are unlikely to outcompete older residents, many offspring may be forced to disperse, exposing themselves to considerable survival risks (Brickhill 1984). For the ageing resident birds, inbreeding and infertility may decrease fecundity, with local extinctions due to random catastrophes remaining a perpetual threat (Brickhill 1987b).

Even where egg predation and low fertility are not a problem, extremely high mortality of chicks following emergence is common to all species (Jones 1988b), an expected consequence of the absence of parental care of hatchlings (Diamond 1983). Although predation is certainly a major cause of these losses (Weir 1973; Jones 1988b), Priddel and Wheeler (1990) have shown that food resources are of critical importance to Malleefowl. By observing chicks released into enclosures of natural vegetation, these authors found supplementary food was necessary to prevent starvation. Chicks provided with apparently natural food supplies were also susceptible to chilling and predation.

These results further emphasize the importance of habitat quality; even in ungrazed and protected locations, environmental conditions may be unsuitable for chick survival. It is probable that the provision of optimal mallee habitats will require some form of manipulative management. For example, Brickhill (1984) found the highest densities of Malleefowl in New South Wales occurring in an area where trees are regularly harvested for eucalypt oil production.



### FUTURE DIRECTIONS

This attempt at providing a comprehensive summary of recent advances in megapode research also highlights areas of ignorance or bias. It is obvious that the majority of work has concentrated on the few Australian species, with relatively few of the other 16 species having been studied in any detail. The extent of our ignorance of even basic ecological information for almost all species is profound. Confronting such a general lack of knowledge at a time when the survival of so many species and populations is uncertain, requires the establishment of priorities of research aims. Of foremost importance should be studies directed toward ensuring adequate conservation of megapode species that are threatened or endangered. In particular, an assessment of the conservation status of the Nicobar Scrubfowl and Bruijn's Brush-turkey is a major priority.

There also remains the pressing need for field data on fundamental ecological and behavioural aspects of all species. Current debates over questions concerning, for example, the evolution of megapode incubation techniques, taxonomic relationships, physiological adaptations, or the behavioural ontogeny of hatchlings, all necessitate imaginative and well planned research programmes. With the sound framework of data now in place upon Frith's foundation, future megapode research promises to be challenging, rewarding, and vital.

### ACKNOWLEDGEMENTS

I appreciate the co-operation of colleagues in the Megapode Specialist Group, especially David Booth, Rene Dekker, and Roger Seymour. Simon Hamlet provided valuable production assistance.

### REFERENCES

- Balout, J. C. and Olson, S. L. (1989). Late Quarternary deposits in New Caledonia. *Smithsonian Contr. Zool.* **469**, 38 pp.
- Baltin, S. (1969). Zur biologie und ethologie des Talegalla — Huhns (*Alectura lathami* Gray) anther besonderer Berücksichtigung des Verhaltens während der Brutperiode. *Z. Tierpsychol.* **26**: 524–572.
- Barrett, C. and Crandal, L. S. (1931). Avian mound builders and their mounds. *New York Zool. Soc. Bull.* **34**: 106–127.
- Beehler, B. M., Pratt, T. K. and Zimmerman, D. A. (1986). *Birds of New Guinea*. (Princeton University Press, Princeton.)
- Bishop, K. D. (1980). Birds of the Volcanoes — the scrubfowl of West New Britain. *World Pheasant Assoc.* **5**: 80–90.
- Blakers, M., Davies, S. J. J. F. and Reilly, P. N. (1984). 'The Atlas of Australian Birds'. (Melbourne University Press: Carlton.)
- Bohner, J. and Immehnann, K. (1987). Aufbau, Variabilität und mögliche Funktionen des Rufduetts beim Thermometerhuhn *Leipoa ocellata*. *J. Ornith.* **128**: 91–100.
- Booth, D. T. (1984). Thermoregulation in neonate malleefowl (*Leipoa ocellata*). *Physiol. Zool.* **57**: 251–260.
- Booth, D. T. (1985). Thermoregulation in neonate brush-turkeys (*Alectura lathami*). *Physiol. Zool.* **58**: 374–379.
- Booth, D. T. (1987). Home range and hatching success of malleefowl *Leipoa ocellata* Gould (Megapodiidae). in Murray mallee near Renmark, S.A. *Aust. Wildl. Res.* **14**: 95–104.
- Booth, D. T. (1988). Shell thickness in megapode eggs. *Megapode Newsl.* **2**: 13.
- Booth, D. T. and Seymour, R. S. (1987). Effects of eggshell thinning on water vapor conductance of Malleefowl (*Leipoa ocellata*) eggs. *Condor* **89**: 453–459.
- Brickhill, J. (1984). Malleefowl. A remarkable bird with an uncertain future. *Aust. Nat. Hist.* **21**: 147–151.
- Brickhill, J. (1985). An aerial survey of nests of malleefowl *Leipoa ocellata* Gould (Megapodiidae) in central New South Wales. *Aust. Wildl. Res.* **12**: 257–261.
- Brickhill, J. (1987a). The conservation status of Malleefowl in New South Wales. Masters Natural Resources thesis, University of New England, Armidale, Australia.
- Brickhill, J. (1987b). Breeding success of Malleefowl *Leipoa ocellata* in central New South Wales. *Emu* **87**: 42–45.
- Broome, L. S., Bishop, K. D. and Anderson, D. R. (1984). Population density and habitat use by *Megapodius freycineti eremita* in West New Britain. *Aust. Wildl. Res.* **11**: 161–171.
- Clark, G. A. (1960). Notes on the embryology and evolution of the Megapodes (Aves: Galliformes). *Yale Peabody Mus. Postilla* **45**: 1–7.
- Clark, G. A. (1964a). Ontogeny and evolution in the Megapodes (Aves: Galliformes). *Yale Peabody Mus. Postilla* **78**: 1–37.
- Clark, G. A. (1964b). Life histories and the evolution of megapodes. *Living Bird* **3**: 149–167.
- Coates, B. J. (1985). 'The Birds of Papua New Guinea' Vol. 1. (Dove Publishing, Brisbane.)
- Coles, C. (1937). Some observations on the habits of the brush-turkey. *Proc. Zool. Soc. (Lond.)* **107**: 261–273.
- Cracraft, J. (1973). Continental drift, paleoclimatology, and the evolution and biogeography of birds. *J. Zool. Lond.* **169**: 455–545.
- Crome, F. H. J. and Brown, H. E. (1979). Notes on the social organization and breeding of the Orange-footed Scrubfowl *Megapodius reinwardt*. *Emu* **79**: 111–119.
- Dekker, R. W. R. J. (1988a). English names of Megapodes. *Megapode Newsl.* **2**: 2–3.
- Dekker, R. W. R. J. (1988b). Notes on ground temperatures at nesting sites of the Malleo *Macrocephalon malleo* (Megapodiidae). *Emu* **88**: 124–127.
- Dekker, R. W. R. J. (1989). Predation and western limits of megapode distribution (Megapodiidae: Aves). *J. Biogeog.* **16**: 317–321.
- Diamond, J. (1983). The reproductive biology of mound-building birds. *Nature* **301**: 288–289.
- Dow, D. D. (1980). Primitive weaponry in birds: Australian Brush-turkey's defence. *Emu* **80**: 91–92.

- Fleay, D. H. (1937). Nesting habits of the Brush-turkey. *Emu* 36: 153-163.
- Frith, H. J. (1956a). Breeding habits of the family Megapodiidae. *Ibis* 98: 620-640.
- Frith, H. J. (1956b). Temperature regulation in the nesting mounds of the Malleefowl, *Leipoa ocellata* Gould. *C.S.I.R.O. Wildl. Res.* 1: 79-95.
- Frith, H. J. (1957). Experiments on the control of temperature in the mound of the Malleefowl *Leipoa ocellata* Gould (Megapodiidae). *C.S.I.R.O. Wildl. Res.* 2: 101-110.
- Frith, H. J. (1959a). Incubator birds. *Sci. Am.* 201(2): 52-58.
- Frith, H. J. (1959b). Breeding of the Malleefowl, *Leipoa ocellata* Gould (Megapodiidae). *C.S.I.R.O. Wildl. Res.* 4: 31-60.
- Frith, H. J. (1962a). 'The Malleefowl'. (Angus & Robertson: Sydney.)
- Frith, H. J. (1962b). Conservation of the Malleefowl, *Leipoa ocellata* Gould (Megapodiidae). *C.S.I.R.O. Wildl. Res.* 7: 33-49.
- Gould, J. (1865). 'Handbook to the Birds of Australia'. Vol. II. (The Author, London.)
- Immelmann, K. and Bohner, J. (1984). Beobachtungen am Thermometerhuhn (*Leipoa ocellata*) in Australien. *J. Ornith.* 125: 141-155.
- Jones, D. N. (1987). Behavioural ecology of reproduction in the Australian Brush-turkey *Alectura lathami*. Ph.D. Thesis, Griffith University, Nathan, Australia.
- Jones, D. N. (1988a). Selection of incubation mound sites by the Australian Brush-turkey *Alectura lathami*. *Ibis* 130: 251-260.
- Jones, D. N. (1988b). Hatching success of the Australian Brush-turkey *Alectura lathami* in south-east Queensland. *Emu* 88: 260-262.
- Jones, D. N. (1988c). Construction and maintenance of the incubation mounds of the Australian Brush-turkey *Alectura lathami*. *Emu* 88: 210-218.
- Jones, D. N. (1989). Mounds and mates. The breeding strategies of the Australian Brush-turkey. *Aust. Sci. Mag.* 31(2): 13-16.
- Jones, D. N. (1990). Social organization and sexual interactions among male and female Australian Brush-turkeys, *Alectura lathami*. *Ethology* (in press).
- Kloska, C. and Nicolai, J. (1988). Fortpflanzungsverhalten des Kauni-Talegalla (*Aepyodius arfakianus* Salvad.) *J. Ornith.* 129: 185-204.
- Kimber, R. G. (1985). The history of Malleefowl in central Australia. *R.A.O.U. Newsl.* 64: 6-8.
- Lincoln, G. A. (1974). Predation of incubator birds (*Megapodius fregineta*) by Komodo dragons (*Varanus komodoensis*). *J. Zool. Lond.* 174: 419-428.
- Lister, J. J. (1911). The distribution of the Avian genus *Megapodius* in the Pacific Islands. *Proc. Zool. Soc. Lond.* 52: 749-759.
- Mackinnon, J. (1978). Sulawesi Megapodes. *World Pheasant Assoc. J.* 3: 96-103.
- Mackinnon, J. (1981). Methods for the conservation of maleo birds, *Macrocephalon maleo* on the island of Sulawesi, Indonesia. *Biol. Cons.* 20: 183-193.
- Maynard Smith, J. (1984). The ecology of sex in 'Behavioural Ecology. An Evolutionary Approach'. (eds. J. R. Krebs and B. Davies), pp. 201-221. (Blackwell: Oxford.)
- Megapode Specialist Group. (1988). Megapodes under threat. *Megapode Newsl.* 2: 17-18.
- Nice, M. M. (1962). Development of behaviour in precocial birds. *Trans. Linnean Soc. New York* 8: 1-211.
- Olson, S. L. (1980). The significance of the distribution of the Megapodiidae. *Emu* 80: 21-24.
- Olson, S. L. (1985). The fossil record of birds in 'Avian Biology' (eds. D. S. Farner, J. R. King and K. C. Parkes), Vol. 8, pp. 80-238. (Academic Press: New York.)
- Priddel, D. and Wheeler, R. (1990). Survival of Malleefowl chicks in the absence of ground-dwelling predators. *Emu* (in press).
- Rich, P. V. and van Tets, C. F. (1985). 'Kadimakara — Extinct Vertebrates of Australia'. (Pioneer Design Studio: Lilydale.)
- Ripley, S. D. (1960). Distribution and niche differentiation in species of Megapodes in the Moluccas and Western Papuan area. *Proc. 17th Int. Ornith. Cong.*, 631-640.
- Rinke, D. (1986). Notes on the avifauna of Nivaloo Island, Kingdom of Tonga. *Emu* 86: 82-86.
- Seymour, R. S. (1984). Patterns of lung aeration in the perinatal period of domestic fowl and Brush-turkey in 'Respiration and Metabolism of Embryonic Vertebrates'. (ed. by R. S. Seymour) pp. 319-332. (Junk: Dordrecht.)
- Seymour, R. S. (1985). Physiology of Megapode eggs and incubation mounds. *Proc. 18th Int. Ornith. Cong.* 854-863.
- Seymour, R. S. and Ackerman, R. A. (1980). Adaptations to underground nesting in birds and reptiles. *Am. Zool.* 20: 437-447.
- Seymour, R. S. and Rahn, H. (1978). Gas conductance in the eggshell of the mound-building Brush-turkey. in 'Respiratory Function in Birds. Adult and Embryonic'. (ed. J. Piper) pp. 241-246. (Springer-Verlag: Berlin.)
- Seymour, R. S., Vleck, D. and Vleck, C. M. (1986). Gas exchange in the incubation mounds of megapode birds. *J. Comp. Physiol. B.* 156: 773-782.
- Seymour, R. S., Vleck, D., Vleck, C. M. and Booth, D. T. (1987). Water relations of buried eggs of mound building birds. *J. Comp. Physiol. B.* 157: 413-442.
- Sibley, C. S., Ahlquist, J. E. and Monroe, B. L. (1988). A classification of the living birds of the World based on DNA-DNA hybridization studies. *Auk* 105: 409-423.
- Stark, J. M. (1988). Note on the skull morphology of *Macrocephalon maleo*. *Megapode Newsl.* 2: 5-7.
- Sturkie, P. D. (1976). 'Avian Physiology'. (Springer-Verlag: New York.)
- Todd, D. (1983). Pritchard's Megapode on Niuafoou Island, Kingdom of Tonga. *World Pheasant Assoc. J.* 8: 69-88.
- Trivers, R. L. (1972). Parental investment and sexual selection in 'Sexual Selection and the Descent of Man'. (ed. B. Campbell) pp. 136-179. (Aldine: Chicago.)
- Vleck, D., Vleck, C. M. and Seymour, R. S. (1984). Energetics of embryonic development in the megapode birds, malleefowl *Leipoa ocellata* and brush-turkey *Alectura lathami*. *Physiol. Zool.* 57: 444-456.
- Weathers, W., Weathers, D. L. and Seymour, R. S. (1990). Polygyny and reproductive effort in the Malleefowl *Leipoa ocellata*. *Emu* (in press).
- Weir, D. G. (1973). Status and habits of *Megapodius pritchardii*. *Wilson Bull.* 85: 79-82.
- White, C. M. N. and Bruce, M. B. (1986). 'The Birds of Wallacea'. (Brit. Ornithol. Union: London.)