Megapodes: A fascinating incubation strategy

Cagan H Sekercioglu
University of Utah

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Megapodes are large, terrestrial, galliform birds that have the most precocial chicks among all bird groups. This is made possible by their eggs being buried either in areas that are naturally warm, such as decaying tree roots, geothermally-heated soil and beaches exposed to solar radiation, or in homeothermic mounds of vegetation and earth constructed and maintained by the parents. These large mounds (up to 5 meters in height) are thermally stable and require little maintainance in most species. The utilization of natural heat sources has meant long incubation times for the eggs, and combined with the adaptations of the egg and the embryo, the chicks are fully developed and completely independent upon hatching. They are many times heavier than the chicks of related birds of similar adult size, are able to extricate themselves from the nest mound without any adult help and can fly within an hour. Megapodes are released from the associated costs and constraints associated with parenthood. This unique breeding strategy has affected many aspects of megapode behavior and physiology, making them the subjects of many studies. Mainly limited to the humid tropical forests of Australasia and Philippines, 11 of 21 megapode species are considered globally threatened as a result of habitat destruction, hunting, egg poaching and introduced predators. Urgent measures need to be taken to prevent imminent extinction of these fascinating birds.

The class Aves is known for the relative uniformity of the biology of its members. Even though there are more than 9,700 species,[1] birds are much less divergent in terms of their anatomical and physiological structure than many comparable groups, such as mammals or reptiles (in the traditional sense). This is mainly a consequence of the high degree of specialization necessary for an aerial way of living. Many of the specializations required are so severe and so integral to the avian biological structure that they have prevented the extensive divergence of even the flightless forms.

This uniformity is especially true for avian reproductive biology. While many vertebrate groups display a wide range of forms of reproduction, from oviparity to viviparity, birds are oviparous without exception, and almost all of the species incubate their eggs by using the warmth of their bodies. This is true for many species that live in habitats with environmental extremes, such as the Emperor Penguin *Aptenodytes forsteri*, which incubates its single egg in the freezing winter of Antarctica, braving storms with temperatures that reach -70° C. It provides the necessary warmth for the egg by balancing it on its feet and covering it with a flap of belly skin for over a month.[2]

There is one remarkable group of birds, however, that provides an exception to incubation using body heat. These are the megapodes belonging to the Australasian family Megapodiidae, the members of which use environmental heat sources to incubate their eggs.[3,4,5] There are 19 species of omnivorous galliforms that mainly prefer closed tropical vegetation.[2] The heat sources they utilize include solar-heated sand, geothermal heat and most importantly, microbial respiration generated through the building of mounds of vegetation and leaf litter.[3,5,6] Even though incubation using solar-heated beaches and volcanic and other geothermal sources does not require very much work besides finding a suitable incubation site, the construction and maintenance of incubation mounds usually involves extensive labor, mainly by the male, including the collecting of up to 7 tons of leaf litter and vegetation.[2,7] In addition, in some species such as the Malleefowl *Leipoa ocellata*, the mound is tended carefully for up to 11 months, mainly in order to of regulate the temperature and relative gas pressures inside the microenvironment of the mound.[2,5] Females of this family usually lay very large clutches, composed of eggs that are significantly (up to three times) larger than the expected size, with high yolk content

Cagan Sekercioglu graduated from Harvard University in 1997 with a degree in Anthropology and Biology. He is currently pursuing his Ph.D. at the Center for Conservation Biology at Stanford University.

and low water content, which contributes to the formation of highly-developed chicks.[8] There is no parental care, however, and once the chicks, which are the most precocious in the avian world,[9] have hatched and have left the mound, they are completely on their own.[2]

Evolution and Phylogeny of Megapodes

Even though it has been argued that the megapodes descended directly from reptiles,[4] especially since megapodes share some of their incubation behavior with crocodiles and turtles,[10] today it is definitely known that the environmental incubation is a synapomorphic trait. Based on evidence from anatomy, karyology, egg white proteins, mallophagan (feather lice) taxa, and DNA-DNA hybridization, the megapodes are currently considered to form a very distinctive monophyletic family within the Galliformes.[3,4] There is still controversy, however, on the relationships of the megapodes to other galliforms. The Cracidae (guans, chachalacas, etc.), the next clearly defined family in the Galliformes, seems to be related to the megapodes based on some evidence from musculature of the wing, DNA-DNA hybridization, and anatomy (such as the hallux being even with the ground in both groups, in contrast to the rest of the Galliformes). Other studies, including those of osteology, feather microstructure, eggshell structure, egg-white proteins, uropygial gland secretions, and feather lice, however, suggest that the megapodes, rather than being the sister group of the cracids, are the sister group of all non-megapode Galliformes, with one suborder each alloted to the megapodes, the cracids, and the rest of the Galliformes. The present consensus favors the latter taxonomy.[2,4]

The current intrafamilial phylogeny usually divides the megapodes into three subfamilies. The first group includes the brush turkey genera *Alectura* (monotypic), *Aedypodius* (two species) and *Talegalla* (three species; this genus is sometimes considered more closely related to the malleefowl, *Leipoa ocellata*), which are eutaxic mound-builders with a naked uropygial gland. The second is the monotypic *Leipoa ocellata* , with similar morphology and habits, but distinctive in being the only megapode that is adapted to semi-arid and arid environments. Finally come the scrubfowl, containing the genera *Megapodius* (eleven species) and the monotypic *Eulipoa*. The scrubfowl are diastataxic (fifth secondary feather of the wing being absent), have a naked uropygial gland, and exhibit the whole range of megapode incubation behavior from mound building to laying eggs in geothermal sites. Finally,there is the monotypic genus *Macrocephalon*, the Maleo, which is similar to the scrubfowl and is an obligate burrow nester.[2,4]

Geographical Origin and Present Distribution

There is an ongoing controversy over the geographical origin of the megapodes. While Olson[11] argues for a late-Miocene origin in North America, which is regarded by some researchers as the center of diversity for the cracids,[11] others, such as Cracraft,[12] support a Gondwanan origin for the order Galliformes, with the separation of the cracids and megapodes taking place after the breakup of the super-continent. The supporters of this theory argue that a proto-megapode group dispersed into Australia via Antarctica and the family originated within Australia.[2,3]

The present distribution of the megapodes is largely to the east of the Wallace's line, with greatest diversity in the Australo-Papuan Subregion. There is only one representative, the Nicobar Scrubfowl *Megapodius nicobarensis*, in Asia. There are two competing explanations for this distribution. One is that the significant presence of other galliforms, especially the Phasianidae in Asia, has resulted in the competitive exclusion of the megapodes from that region.[11] An even more significant reason could be the marked increase in the diversity and abundance of many mammalian predators in the area that is not occupied by the megapodes.[13] The breeding behavior of especially the mound-building megapodes, with their conspicuous mounds that need to be constructed and tended by the parents, would attract many predators and egg predators, excluding the megapodes from areas with a high density of mammalian predators. The burrow-nesting megapodes might have an advantage in that respect, since they rarely visit their nesting grounds after the laying of the eggs.[13] The hypothesis that at least the mound-building megapodes are excluded from areas that host mammalian predators is supported by some interesting distribution patterns, such as the absence of the Orange-footed Scrubfowl *Megapodius freynicet* from the main island of the Kangean Archipelago of Indonesia, on which there are leopards and civets, while the same species occurs on the surrounding islands that do not support these predators.[2]

Evolution of Incubation

The most significant event in the phylogenetic history of the megapodes is considered to be the evolution of the incubation method.[4] Again, there are conflicting ideas as to the direction and the mechanism of the origin of this unique strategy. One hypothesis is that burrow-nesting evolved first since it is simpler than the building of elaborate mounds. Supporters of this idea argue that the "proto-megapode" made use of external heat sources, such as volcanically heated earth, by nesting over them. In time, the birds lost the ability to do any incubation without relying on an environmental heat source, and as the patterns of volcanism changed, some were forced to build mounds of vegetation in order to regulate the incubation temperature.[3,4]

Presently, however, the general consensus supports the alternative theory that argues for mound building evolving first, followed by burrow-nesting. Since mound-building is displayed by four of the six extant genera, burrow-nesting evolving first would mean that four genera later lost this habit and started to build mounds. It is more parsimonious if mound-building evolved first. In addition, the foot structure of the burrow-nesting Maleo *Macrocephalon maleo* is more advanced than the rest of the megapodes with respect to digging, and the eggs of the genera *Macrocephalon* and *Megapodius* contain significantly more yolk (61% to 69% in *Macrocephalon*) than the eggs of the rest of the megapodes (48-55%), which is considered to be another derived trait.[2,15]

There is also evidence from the rest of the avian world as to how mound-building might have evolved initially. Tinamous (Tinamidae), which are primitive, paleognathous, terrestrial birds thought to be related to the galliforms, cover their eggs with leaves when they leave the nest in order to keep them warm and inconspicuous to predators.[2] The Egyptian Plover *Pluvianus egyptianus* covers its eggs with 2-3 mm of sand during the day, and incubates over the sand, at night uncovering the eggs and incubating them in direct contact with its body.[10] This method very likely evolved as a way to hide the eggs during the day, secondarily serving as insulation from very high temperatures prevalent in a desert environment. It is not difficult to imagine the megapodes using the same strategy for the concealment of their eggs, with more and more vegetal material being added on to the eggs as the birds "discovered" that they could incubate their eggs using this method.

Later on, some of the tropical forest mound-builders might have laid their eggs between the decaying roots of

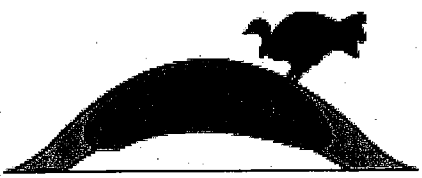

Figure 1. The Australian Megapode. Once thought to be descendents of reptiles, the megapode expresses the synapomorphic trait of using environmental heat sources to incubate their eggs.

trees, as seen in several *Megapodius* species that use the heat generated by the decaying wood. It is also possible that some individuals started laying their eggs in the soil of some volcanically heated sites in the tropical forest, which led the way to laying eggs in solar-heated beaches.[16] Thus, the evolution of the environmental incubation behavior in megapodes probably followed a direction from mounds in the rainforest to simple holes dug in exposed tropical beaches.

Mound Structure and Function

Of the whole range of incubation strategies megapodes display, the most distinctive and labor-intensive is the construction of large vegetation mounds. These impressive structures sometimes reach 20m in diameter and 2m in height, containing over 7 tons of material in the yearly-constructed mounds of the Australian Brush Turkey *Alectura lathami*.[10] The mounds of the Orange-footed Scrubfowl *Megapodius reindwardt*, which sometimes build their mounds on top of previous mounds, may reach 8m in height, 51m in diameter and probably contain over 100m^3 of material weighing over 50 tons.[2] Jones[17] found that *Alectura* significantly preferred closed canopy to more open areas and also preferred areas with high undergrowth, such as with a dense cover of *Lantana* spp. Areas with more canopy cover provide more leaf litter for the construction of the mound, as well as protect the mound from excessive water loss, and all other mound-building megapodes, except for the *Leipoa ocellata* , seem to prefer closed tropical forest habitats, which makes it likely that this was the original habitat of the family.[2]

Heat is generated in the vegetation mounds by the respiration of microorganisms, especially decomposer thermophilic fungi, with *Penicillium* sp. being the most common.[2,18] It is thought that once past the construction phase, the mounds are "stable homeotherms,"[18,19] that reach an equilibrium temperature very close to 33°C, and any significant short-term fluctuations from this temperature (such as those caused by opening of the mound or by daily fluctuations of the ambient temperature) are balanced by differences in heat loss and heat production and the mound returns to the equilibrium temperature. The birds are thought to test the temperature of the mounds by making use of the heat-sensitive areas on their necks, heads, and inside their mouths, and if there are any significant changes in temperature or gas ratios, leaf litter is added or ventilation holes are opened for regulation.[20] Experiments have shown that, at least in *Leipoa ocellata* , the temperature regulation is accurate up to 1°C.[21]

To reach the equilibrium temperature, the mounds need to exceed a critical size and they must also have a critical water content to minimize heat conductivity and microbial heat production. Artificial mounds that were over 0.75m high and two meters wide were found to generate the necessary heat for incubation,[19] and for the Australian Brush Turkey *Alectura lathami* mounds on Kangaroo Island, Seymour and Bradford[18] found the critical mass as being close to 3,000 kg . The temperature of the mound is subject to change depending on the characteristics of the site, especially with respect to the temperature and rainfall regimes, and the composition of the leaf

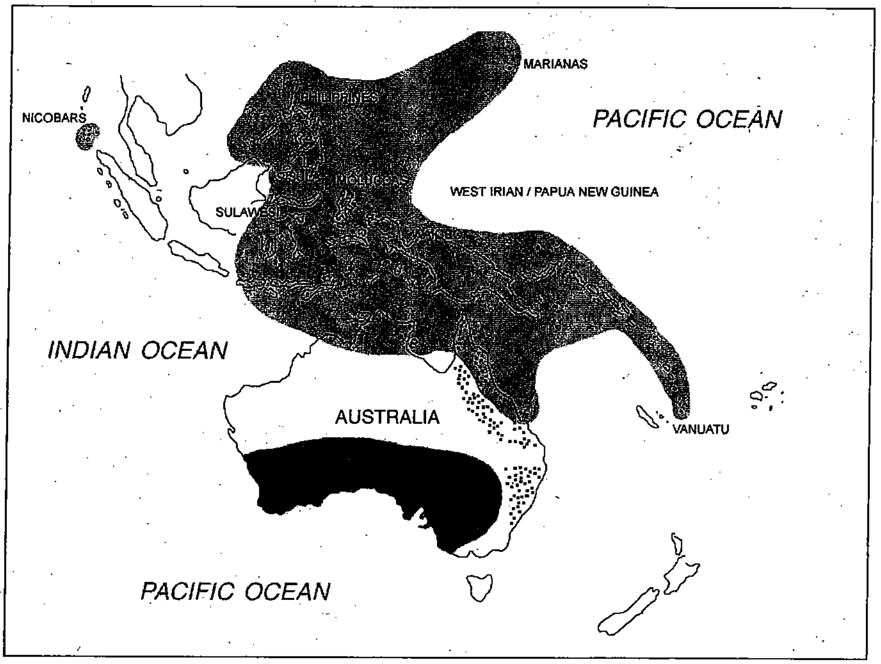

Figure 2. Distribution of Megapodiidae. The light gray area represents the distribution of the genus *Megapodius*; the dark grey area represents the distribution of *Leipoa*; the dotted area represents the distribution of *Alectura*.

litter. The mounds of *Alectura lathami* have a layer of coarse sticks on the surface, which is presumed to trap air on the surface, further insulating the mound.[6] Occasional mixing is required in order to raise the oxygen level, to let off excess carbon dioxide, to prevent compaction, to keep thermal conductivity low, and to distribute the decomposers evenly.[2,18] Recently constructed mounds are also occasionally opened by the males in order to prevent build up of excessive heat, which wastes energy and can kill the eggs.[2]

The water content of the mound is also crucial. If there is not enough moisture in the mound, the eggs can rapidly dehydrate, and during major droughts there have been mass mortalities of megapode broods. High water content is also avoided by the birds, since wet mounds not only are less homeothermic, but also the gas tensions (especially O_2 and CO_2) in the mound reach lethal levels if the water content is high.[18,22] Seymour and Bradford[18] have discovered that in *Alectura* mounds the critical water content was more than 0.2ml/g of dry material, usually averaging 0.3ml/g in the natural mounds.

The characteristic tending and raking of the mound by the parents, especially by the male, is greatly reduced once the mound is in the maintenance phase, except for the Malleefowl *Leipoa ocellata,* whose mounds require more tending due to the highly fluctuating temperatures of its temperate, arid environment.[5] Since *Leipoa ocellata* use a combination of solar heat and heat from decomposition, the significance of solar heat increases as the season progresses from spring to summer, and depending on the season, the male can be seen to be insulating the mound with sand, opening the mound to let off excess heat, or even spreading sand to warm under the sun during the day, and at night covering the mound with the sun-heated sand. Frith[5] experimented with a buried electric heater powered by a remote generator in the mound of a Malleefowl. When he heated the mound in the spring, the bird opened the mound to let off excess heat, probably assuming that it was generated by excessive microbial decomposition. When the same experiment was repeated in the summer, however, the bird covered the mound with sand in order to insulate it, very likely based on the assumption that the heating of the mound was because of too much sun.[21] Since the thermal conductivity of sand is higher than leaf litter and decaying vegetation, the *Leipoa ocellata* mound is less prone to overheating as well as to dehydration at a given temperature than the vegetation mounds.[23] This is highly adaptive because of the extreme temperatures experienced in the arid, open habitat.

For *Alectura lathami* and the other mound-building megapodes, however, the work required past the construction phase is much less. Seymour and Bradford[18] discovered that once past the equilibrium size, 1 cm of litter could raise the temperature of the *Alectura lathami* mound as much as 1.5°C. Jones[24] found that male *Alectura lathami* in Queensland tend their mounds for an average of only half an hour every day, whereas evidence from Kangaroo Island indicates that the mounds can be left for days at a time and still remain around the incubation temperature.[18] This is obviously a great advantage for the birds involved, leaving them free to forage or even mate multiple times. Even more important is the fact that an average mound generates far more heat (about 20 times more for *Alectura lathami*) than an incubating bird, making possible the incubation of a much larger clutch than would be possible if the bird were to incubate it physically.[18]

Burrow Nesting and Brood Parasitism

The second major incubation strategy of megapodes is that of burying their eggs in burrows in the ground and exploiting some naturally occurring sources of heat, a method that requires substantially less work.[4] There are three different forms of this strategy, where the species involved bury their eggs between the decaying roots of trees (such as the Vanuatu Scrubfowl *Megapodius layardi*), in volcanically-heated soil, and in sun-exposed beaches.[4] Since good nesting sites are scarce, some of the burrow nesters use communal incubation sites that are visited by the birds only when they need to lay their eggs, after which the eggs are on their own. For example, at Polikilli in New Britain, Papua New Guinea, there are tens of thousands of mounds and 53,000 birds were estimated to have been present during one breeding season.[2] Since burrow-nesters usually leave immediately after laying their eggs and are unable to regulate the heat of the burrow, they choose sites where the temperature is relatively constant. In fact, incubation sites of some of the burrow-nesting species such as the Maleo *Macrocephalon maleo* were found to exhibit very similar temperatures to the mounds of the mound-building species.[25] In fact, one way of burrow-nesting, that of laying eggs in rotting tree stumps is very similar to mound-building in that it also uses the heat of rotting vegetation, but in a passive way.[2]

Mound parasitism is also observed in megapodes, even though it has been studied very little. For example, eggs of the Dusky Scrubfowl *Megapodius freynicet* have been found in the mounds of other individuals of the same species, as well as those of *Talegalla* spp. and Wattled Brush Turkey *Aepypodius arfakianus*.[21,26] More examples of mound parasitism are discovered regularly,[2] and it is an area in which there is a significant potential for original research.

Mating Systems and Pair Bonding Patterns of the Megapodes

Another very interesting aspect of the breeding behavior of the megapodes is the question of pair-bonding and certainty of paternity in the mound-building megapodes. Given the great effort expanded by the males of the mound-building species and based on observations of a number of species in the wild and in zoos, the mound-building megapodes were thought to be universally monogamous.[5,20,27] However, recent evidence, especially from *Alectura lathami* shows that this may not be so. Given the extensive investment by the male, how is it possible that he can tolerate cuckoldry? The answer to that question has been supplied by the detailed studies of Jones, who found that *A. lathami* are promiscuous, and a significant secondary function of the mounds is to attract females.[6,15,24] Jones and Birks[20] observed that since females assessed the condition of the mounds, males without mounds were never successful in reproducing, and the building and the constant maintenance of incubation mounds was essential in order to attract females and to inseminate them. As a result, the males do not defend the females but vigorously defend their mounds against any usurpers. Since the mound provides far more heat than the average clutch requires, the male *A. lathami* tolerates to some degree the possible presence of eggs inseminated by another male since their presence does not reduce the reproductive output of the male.[20] Even so, the male *A. lathami* is often observed to harass the female immediately after copulation, likely in order to prevent her from laying her eggs immediately, which is a definite sign that they were inseminated by another male since there was not sufficient time for the eggs to be inseminated by the sperm of the mound's owner. By preventing the female from laying her eggs, the male is probably delaying the passage of the egg until his sperm has had time to inseminate.[20] In addition, the aggressive behavior of the male keeps away non-laying females and increases its copulation rate.[28]

Jones[20] has summarized the mating system of the megapodes as female-defense monogamy, resource defense polygyny plus polyandry and resource-defense monogamy. The males of the burrow-nesters and those of species that do not defend their mounds can defend the females because they do not invest in any time necessary to defend a mound. On the other hand, *A. lathami* (and *Aepypodius* spp.) build and defend mounds in order to attract multiple females, which visit multiple mounds and can mate with multiple males.[2]. Finally, *Leipoa ocellata*, which lives in arid areas with very limited resources and low population density, seems to be monogamous.[5] This is mainly a result of the low population density and the small likelihood of encountering other individuals, since *L. ocellata* pairs spend little time together and the social organization of the species resembles that of *A. lathami*.[20] Interestingly, an occurrence of polygyny was observed, where a male simultaneously maintained two mounds and bred with two females in an area with abundant resources, including human-supplied water.[29]

Clutch Size

Since parental care in the form of building and maintaining mounds is mostly done by the males of megapode species, and since there is no parental care of the hatchlings, the female can devote most of its resources to producing a large clutch. The average megapode egg is very large (106x62mm and 231g in *Macrocephalon maleo*,[2] and usually makes up 10-20% of the body mass of the adult female.[2] Vleck,[30] found the eggs of both *Leipoa ocellata* and *Alectura lathami* to average around 180g, which would be three times the expected size for birds of their size. In addition, since there is no restriction on the period of egg-laying, female megapodes are fertile throughout the year, and invest most of their resources in laying very large clutches by maintaining resource balance and egg production.[30] In the wild, a female *Alectura lathami* weighing 1.8 kg laid 3 kg of eggs in a few months,[30] while in captivity the female of this species can lay 30 eggs over a period of several months, representing three times its body weight.[2] This very large clutch size is seen throughout the family. The extended egg-laying season protects the eggs against predation, temporally distributing them, while the large clutch size possibly compensates for the first-year mortality incurred from the lack of any post-hatching parental care. It has been estimated that in *A. lathami*, about 15 hatchlings per year are raised to independence (i.e. hatch and leave the nest).[30]

Adaptations of the Egg and the Embryo to Mound Incubation

The physiological adaptations of the egg are just as impressive. The eggs of megapodes have very high yolk content, second only to that of Kiwi *Apteryx australis*.[8] In the mound-building genera, the yolk content ranges from 48 to 55% of the egg weight, while in the eggs of the burrow-nesters, this ratio is between 61% and 69%.[4] This high yolk content significantly contributes to the extreme precociality of the hatchling. The average yolk content for precocious birds is 35%, and the fact that the ratio of the weight of the hatchling megapodes to that of the fresh egg (64%-70%) being similar to the average for birds (68%) shows that the extra yolk is used for the extremely precocious development of the chicks.[23] High yolk content of the egg also means low water content, and the eggs of megapodes are among the "driest" in the avian world, with an average of 67% water (very similar to the average for adult vertebrates), compared with 75% in other precocial species and 84% in altricial species.[2] Since the humidity of the mound minimizes water loss from the egg (8% of the initial egg weight in *Alectura lathami* is lost as water during incubation),[2] the resources of the egg are concentrated on storing the energy for advance development of the chick. This process of "xerogenic maturation" has been confirmed by Sotherland and Rahn,[8] who found a positive correlation between increased yolk content, decreasing water content and precocious offspring.

The megapode eggs also have important adaptations for the unfavorable oxygen conditions inside the mound. In addition to not being in direct contact with air, the relatively high humidity of the megapode mounds makes the maintenance of favorable gas tensions inside the egg even more difficult, with oxygen levels being as low as 17% near the egg.[22] The shells of the megapode eggs are, on average, 31% thinner than those of similar sized galliforms. This results in a decrease in the energy and resources used to produce an egg, but more importantly, the gas tensions inside the megapode eggs are very similar to those of the eggs of other birds.[20] In addition, the egg shell thins even further towards the end of the incubation period, increasing the gas conductance of the egg as the oxygen need of the embryo increases.[22]

The limited amount of water loss seen in the megapode eggs means that the air space that forms late in the egg incubation of many other birds, enabling the chick to take its first breath prior to hatching, is not present in megapode eggs. As a result, there is no overlap between the chorioallantoic and pulmonary respiration; the transition between them is rapid, and the hatching is explosive. Even though an egg tooth is formed early in the development, it is later lost, and instead, the megapode chick hatches very quickly by kicking its way out of the egg, immediately switching to pulmonary respiration. Once again the thin egg shell provides an advantage, by making it easier for the chick to break out.[2,18,20]

Even though the length of the incubation period of the megapodes varies with respect to the condition of the mound,[2] on average it is 60% longer than the average for other birds.[21] This is obviously required if a "super-precocious" chick is to develop, and it is thought that the high yolk content of the egg enables the chick to get through this long period. The chicks of *Leipoa ocellata* and *Alectura lathami* were observed to have increasing oxygen consumption during incubation, with a leveling in the last week of incubation. This pattern is similar to that of other precocious species, with the high maintenance costs due to early development decreasing towards the end of incubation as a result of a reduction in expensive tissue growth and maturation of the physiological systems.[30] Booth[22] discovered that the transition from ectothermic to endothermic in *A. lathami* and *L. ocellata* takes place inside the egg 3-5 days before hatching, which is unlike any other bird species, and this factor again emphasizes the extreme precociality of the family.

Hatching of the Superprecocious Chick

After hatching, a megapode chick spends a lot of energy and time struggling to get out of the mound, which can take two to three days in the tropical mound-building species.[2] It is obvious that the chicks have to be very developed in order to be successful. At hatching, megapode chicks are highly developed, are very large (wingspan up to half the wingspan of the adult bird)[2] and receive no parental care.[20] Booth[22] found that *A. lathami* and *L. ocellata* chicks have a metabolism in between the averages for the adults and the neonates of other birds. In addition, *A. lathami* chicks could thermoregulate immediately between 10-38°C, and even more in *L. ocellata* (5 hours after hatching, the chicks could thermoregulate at temperatures down to 3°C). They are even capable of flight within a few hours. In fact, a *Megapodius freycinet* chick released by an egg collector flew about a mile before retreating into forest cover,[2] and a *M. reinwardt* chick that was estimated to be a few days old was seen 40 km away from the nearest land, without any signs of exhaustion or stress.[31]

Even though the hatching success is usually very high (87% in 499 eggs of *A. lathami*[32] and 79% in *L. ocellata*,)[22] post-emergence mortality is also high, over 90% for *A. lathami*.[32] Even though in areas with introduced predators, such as dogs, cats, foxes, and pigs, egg predation levels might be a lot higher, the extended period of egg-laying usually prevents substantial losses, and in general most of the offspring mortality is due to post-emergence mortality. This is a combination of the lack of parental care and highly terrestrial habits. In addition, the chicks usually emerge from the mound in an exhausted state, making it very easy for many predatory species to prey on them.[32] Fortunately, the large brood sizes of the megapodes seem to balance these losses.

The evolution of incubation using environmental heat sources in megapodes has had very significant implications in terms of the behavior, physiology and ecology of the family. By emancipating themselves from the necessity of incubating their eggs by sitting on them, as well as from post-hatching parental care, the megapodes have been able to increase their brood size tremendously. This high clutch size of very precocious offspring successfully offsets the high first year mortality seen in many terrestrial galliforms.

There is still a lot of research that needs to be done on this amazing family of birds, and the ecology, evolution, behavior, and physiology of the megapodes will captivate biologists for years to come. Unfortunately, because of their terrestrial habits, the sensitivity of the mounds to canopy cover, and the high susceptibility of the eggs and the chicks to predation by people and by introduced and native predators respectively, the megapodes are threatened throughout their range. If urgent conservation measures are not taken, many megapode species will disappear, and their fascinating breeding behavior will be a thing of the past.

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