PEACOCK-PHEASANTS AND ASIATIC SPURFOWL

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Above: According to some molecular data, the monotypic Painted Moluccan Megapode *(Eulipoa wallacei)* is one of the oldest of extent Megapode genera, and similar to archetypal progenitors from which all extent gallinates have descended.
Photo: Sam Woods.

PART 2

EVOLUTIONARY RELATIONSHIPS OF PEACOCK-PHEASANTS AND THEIR ALLIES

"Evolution on a large scale unfolds, like much of human history, as a succession of dynasties. Organisms possessing common ancestry rise to dominance, expand their geographic ranges, and split into multiple species. Some of the species acquire novel life cycles and ways of life. The groups they replace retreat to relict status, being diminished in scattershot fashion by competition, disease, shifts in climate, or any other environmental change that serves to clear the way for the newcomers. In time the ascendant group itself stalls and begins to fall back. Its species vanish one by one until all are gone. Once in a while, in a minority of groups, a lucky species hits upon a new biological trait that allow it to expand and radiate again, reanimating the cycle of dominance on behalf of its phylogenetic kin." - E. O. Wilson (1992)

A Challenge for the Discipline of Comparative Psychology

If you're interested in peacock-pheasants you've read predictable descriptions of pretty feathers accompanied by photos of males "showing off". Yet so far as comprehensive literature is concerned information on the biology of these birds is mostly lacking. It is often the case that physical characteristics and plumage displays, (especially of males), are

used by researchers trying to work out phylogeny within the Galliformes. This proves problematic when misunderstandings on the form and function of plumage display behaviors, lead to contradictions that tend to muddy our comprehension of the evolutionary history of gallinates.

Let's depart from the well-tread path of courtship antics for a moment and examine some characteristics hard-wired into the DNA of these birds. There are behavioral and ecological commonalities that the oldest species of landfowl share. Gaining a comprehension of what constitutes a primitive versus a derived character is key.

Right: Northern Grey Peacock-pheasant, *Polyplectron bicalcaratum bakeri*, pair engaged in pair-bonding display behaviors. Photo: Peter Stubbs.

Plesiomorphy *is a term applied to a character state that is based on features shared by different groups of biological organisms and inherited from a common ancestor.* The features to which it is applied were formerly called 'primitive'. It is the opposite of derived (apomorphic). For example, all known birds produce and hatch from eggs. We can assume that the common ancestor (endothermic theropods) of every one of the bird orders was likewise oviparous. ***Oviparous*** *animals are those that reproduce by laying eggs, with little or no embryonic development within the mother.* This characteristic of avian reproductive biology can be described as plesiomorphic.

Endothermy (warm-blooded), bipedalism, respiration via air sacs and the presence of feathered integument are likewise plesiomorphic characters shared by birds. Trying to tease out primitive features amongst the Galliformes is a bit more problematic as some of it may appear to be a bit counter-intuitive, at least at the onset. For instance, we have traditionally assumed, based upon principles of the theory of sexual selection, that ornate plumage must be a derived character as the evolutionary history of a species is dictated upon by certain selections that females make upon the quality of a male's plumage. And again, theoretically, males of highly ornamented birds are made more vulnerable to predation due to their being handicapped with ornate plumage. The logic follows that males of adorned species play no role in nesting or chick rearing. It doesn't matter if the notion has been adequately tested for its validity. What matters is that the theory makes a certain amount of intuitive sense and that it does.

Nevertheless, the reproductive biology of peacock-pheasants doesn't substantiate these rational assumptions. Male Polyplectrons are known to select and guard nesting sites and periodically manipulate vegetative debris encircling their nests. They inspect their own egg (s) regularly. Male peacock-pheasants bill feed, brood and nurture their chicks well into the subadult phase. What is more, though on the rarest occasion, males have been known to even assume incubating duties and rear their chicks in the absence of the female. Curiously, sexually dimorphic species of peacock-pheasants in which males exhibit highly elaborate plumage are no less paternal than those species that are relatively unadorned

and non-dimorphic. Observations of four groups of free-ranging peacock-pheasants over several years have led me to question everything I've ever read about plumage displays and more essentially, the **comparative psychology** of birds that bear ornamental plumage. What is apparent from my observations, males regardless of form perform diversionary distraction behaviors in attempts to draw attention away from their nests/chicks and redirect the trajectories of trespassers entering their foraging territories. During these encounters males expand their plumage and perform display behaviors that are essentially identical to those performed in the presences of females while in "courtship display" mode. What is more, the bird expresses these visually arresting and shape-shifting erratic deportments as if in anticipation of some further escalation. It hops it buzzes and forces the viewer to make eye contact. It holds your attention… The paternal male peacock-pheasant thrashes and shimmers in all its arresting beauty like a betta fish before a mirror, eventually launching an assault that is equal parts kamikaze helicopter and perturbed rooster. Once the female is incubating their clutch or brooding chicks, her mate ceases to distinguish from what may or may not be harmful. While in this mode the peacock-pheasant's postural displays and exaggerated movements are decidedly more complex (and sinister) than those performed before females but otherwise identical. If observed closely one may notice the intention signals take on a profoundly different expression. Rather than flirting coyly as they might before a mate, once agitated the protective male peacock-pheasant unleashes its tempestuous fury. It inflicts pain by digging its kicking thorns with the deft precision and murderous intent of a psychopath armed with icepicks. The little tyrants becomes full-time agents provocateur instigating conflict and inciting violence on whatever intrusion that's drawn its ire, be that a gardener's glove, a bowl of goldfish, some hapless tortoise or kitten, any unfortunate creature or object.

Left: Adult pair white-cheeked Palawan peacock-pheasant, *Polyplectron emphanum emphanum,* engaged in pair bonding display behaviors. Photo: Peter Stubbs.

Let's expand upon the parameters a bit. What if we were to ask another few questions - How do female peacock-pheasants determine which males will make the most capable defenders of the nest site? Is it possible that females choose males with the most convincing demonstrations of capacity, aptitude, stamina and intention to *defend*? What more could all these elaborate plumage displays tell us about the evolutionary history of the dimorphic species? How do the behavioral ecologies of the two plumage types, ornate and unadorned, compare?

"Primitive" or "Highly Evolved"

Traditionally naturalists described animals in terms of higher and lower, greater and lesser, lower and higher animals, the primitive and highly evolved. Darwin started the ball rolling in regards to the peacock-pheasant and the peacock.

"If we admit the principle of gradual evolution, there must formerly have existed many species which presented every successive step between the wonderfully elongated tail-coverts of the peacock and the short tail-coverts of all ordinary birds; and again between the magnificent ocelli of the former, and the simpler ocelli or mere coloured spots on other birds; and so with all the other characters of the peacock. Let us look to the allied Gallinaceae for any still-existing gradations. The species and sub-species of Polyplectron inhabit countries adjacent to the native land of the peacock; and they so far resemble this bird that they are sometimes called peacock-pheasants. I am also informed by Mr. Bartlett that they resemble the peacock in their voice and in some of their habits. During the spring the males, as previously described, strut about before the comparatively plain-coloured females, expanding and erecting their tail and wing-feathers, which are ornamented with numerous ocelli.
.. As far, then, as gradation throws light on the steps by which the magnificent train of the peacock has been acquired, hardly anything more is needed. If we picture to ourselves a progenitor of the peacock in an almost exactly intermediate condition between the existing peacock, with his enormously elongated tail-coverts, ornamented with single ocelli, and an ordinary gallinaceous bird with short tail-coverts, merely spotted with some colour, we shall see a bird allied to Polyplectron - that is, with tail-coverts, capable of erection and expansion, ornamented with two partially confluent ocelli, and long enough almost to conceal the tail-feathers, the latter having already partially lost their ocelli. The indentation of the central disc and of the surrounding zones of the ocellus, in both species of peacock, speaks plainly in favour of this view, and is otherwise inexplicable. The males of Polyplectron are no doubt beautiful birds, but their beauty, when viewed from a little distance, cannot be compared with that of the peacock. Many female progenitors of the peacock must, during a long line of descent, have appreciated this superiority; for they have unconsciously, by the continued preference for the most beautiful males, rendered the peacock the most splendid of living birds." **Charles Erasmus Darwin**

If you have a look at your historic ornithological books published prior to the 1990's and search for a species list corresponding to chapters you'll find the unadorned quail, partridge and grouse-like gallinates at the beginning of chronologies that culminates with peafowl. This is because it was conventionally assumed that conservative and discrete plumage represents an ancestral condition from which more elaborately plumaged genera are derived. With the advent of molecular biology we often find the opposite to be the case. In many instances the more ornamented species appear to be the least derived and the unadorned prove to be apomorphic. For instance, the unadorned Sumatran bronze-tailed peacock-pheasant is very recently derived, less than 0.7 million years old, a brand new species in geological age, whilst the stunningly ornate Palawan peacock-pheasant is the oldest of its genus, by several *million* years. The Malayan and Bornean are likewise ancient species and exhibiting elaborately adorned plumage.

Left: Adult male Sumatran bronze-tailed peacock-pheasant, *Polyplectron chalcurum*. The sexes of this species are non-dimorphic. Photo: Tomasz Doron.

The Sumatran bronze-tailed resembles a nondescript partridge with a long, slender, pheasant-like tail. Its close cousin the Mountain peacock-pheasant is similarly muted though significantly less so. It too is essentially non-dimorphic. How is it that the Sumatran and Mountain peacock-pheasants, two of the most recently derived species (Pleistocene-aged) are so modestly plumaged? Shouldn't their plumage be the most sublimely ornamented? Why instead do they appear to be so primitive - the most partridge-like, the most pheasant-like, the least peacock-like of all the *Polyplectron*?

Presently, with information derived from molecular data well established we know in this instance, ornate plumage is not a derived character. It is a primitive condition and this has left more than a few researchers scratching their heads.
In an analogous situation we have our exceedingly familiar if underappreciated and unadorned common crow of the Holarctic region and its similarly unremarkably plumaged Corvid relatives. These birds are relatively young so far as their order is concerned. Conversely, their closest surviving kin, those primitive possibly archetypical relatives are none other than the Paradisaeidae (birds of paradise), which are very probably the most ornately plumaged birds on earth. Major lineages of birds of paradise diverged from one another ~ 30 million years ago within the equatorial Australasian bioregion. This was well underway several million years before the Holarctic region's Corvids had arisen. Our temperate climate adapted lineages diversified into the magpie, rook, raven and jay ~ 20 million years ago. Could it possibly be the case that highly ornate plumage is a plesiomorphic trait, as in an ancestral condition?

There are dozens of species of avian hunting snakes native to New Guinea, which is the apparent centre of distribution of the diverse and truly astonishing Paradisaeidae. Just one species, the brown tree snake *Boiga irregularis*, was inadvertently introduced (in the 1950's) to the remote Pacific island of Guam from the Australasian bioregion. Like most species of its genus, *Boiga irregularis* is venomous and often hunts at night. The native birds of Guam had never known tree snakes in all their evolutionary history on the island, and as such had not adapted with anti-predatory defenses to survive them.

**Left: Brown tree snake *Boiga irregularis.* Subtropical Colubrid snakes prey heavily on birds, their eggs and chicks.
Photo: PD-USGOV-INTERIOR-NPS.**

A blink of an eye later and this scourge of arboreal serpents has absolutely decimated the entire assemblage of native bird and other faunal species of this remote Pacific island. This is a genuine ecological disaster. Now that the brown tree snake has run out of native birds to consume they are adapting to a different mode of life regularly descending from the jungle canopy to take young poultry from the ground, even invading houses searching for prey. A rat won't be missed, good riddance! But a kitten or puppy, a golf ball? It's as if there's nothing these serpents won't attempt to kill and eat.

Given the molecular age of **Colubridae** and **Paradisaedae** the cat-eyed, rear-fanged serpent and the ludicrously adorned Corvid, it can be safely assumed that these two ancient lineages: ectothermic reptile and endothermic avian theropod, have shared the majority of their evolutionary history together.

Right: Temperate climate adapted Corvines. Photo: Mark Vaughn.

With such a great diversity of arboreal, venomous bird hunting reptiles in the rain forests of New Guinea, wouldn't the birds of paradise be better off without all their gaudy ornaments? How do birds of paradise avoid being predated upon by tree snakes?

Left: Adult male Raggiana Bird of Paradise *Paradisaea raggiana.* Elongated plumes and expansive coverts with disintegrated barbules like those of the bird of paradise and peacock present a real hazard, as reptiles are incapable of removing plumage before swallowing their prey.
Photo: Denise Menias.

If the present day Australasian bioregion's subtropics are anything like those of the Oligocene period, when the Corvids and Colubrids are believed to have arisen, they will logically harbour a diversity of lineages representing original reptilian and avian fauna. We might expect that interactions between some of the archaic surviving species are not unlike those of their most ancient ancestors that existed in epochs long before most mammalian predators had come into existence. Conversely, a half a world away from the equator, bioregions like the Holarctic had lost entirely their formerly widespread subtropical ecosystems, which could presumably support a diversity of arboreal reptilian bird hunters. Theoretically speaking, without this class of predators present the temperate-adapted Corvids no longer required armaments that shielded the birds against snake strike. If the original Holarctic Corvids were as wonky and colourful as their older Australasian progenitors, it required at least 5-10 million years for them to dress down to their current, cold insulative and otherwise practical attire.

It may be the case that natural selection of elaborately plumaged avian species is one that's been literally shaped by an ancient arms race waged between ectothermic reptiles and endothermic theropods ongoing since at least the Jurassic epoch. Fossils of several long-extinct theropods have recently come to light with plentiful, apparently non-functional (for flight) plumage. A narrative often voiced by investigators regarding these bird-like dinosaurs' unusual integument, is primarily discussed within an intraspecific context, i.e., *these fossil species had ornamental feathering = attracting a mate.* Interspecific encounters between bird-like, though thoroughly flightless and feathered theropod and predatory dinosaur are generally absent from that narrative or at least not discussed in print. Artful depictions of feathered dinosaurs interacting with one another or a predatory species often reveal a level of misunderstanding concerning the form and function of display plumage. A reconstructed fossil species is generally depicted with gaping maw frozen in that life and dead moment when something terrifying is bearing down upon it; or two furiously stupid creatures motion at one another like oversexed Accipitrid nestlings. Artfully rendered feathered wings and tails are just prominent enough to remind one of a Victorian ladies hat. Feathers are pretty and soft and fragile. Birds are frail. Everybody knows peacocks are vainglorious. Ornamented = form without viable function.

Arboreal reptiles are primary predators of a wide diversity of birds unique to the Australasian biogeographic region (The centre of distribution of the birds of paradise and Megapodes). It could be inferred that elaborate plumage and stereotyped display behaviors may provide the so adorned with selective advantages.

Right: Tree Snake.
Photo: Cornell University.

A venomous tree snake emboldened with hunger, after not having eaten since its last meal two months earlier, detects the presence of some tasty Aves resting within the crown of a fruiting forest giant. It raises its head for a better look identifying an assumedly unremarkable starling-sized bird of optimal proportions for a quick and solid meal. The unusually keen-eyed serpent approaches, inching imperceptibly closer all the while gauging how to best strike and subjugate this avian morsel. Some subtle cue alerts the bird that something unpleasant is impending and adjusting its eyes it suddenly recognizes this reptile that's materialized before it. How does the bird react? Does it flee, allowing itself to become displaced from an invaluable (and scarce) food larder, or worse captured with one strike projected with marked precision by the serpent? Not incidentally a bird caught unawares and flying away is precisely what the Colubrid snake is hoping for as it specializes in capturing creatures in mid-flight. Or, does the bird hold its ground refusing to give the serpent an opportunity to make that attempt? Does it hang upside down expanding filamentous flank coverts shielding its vulnerable thighs and mantle as we observe in the antics of lekking species of *Paradisaea*? With as many dozens of diverse species of birds of paradise endemic to the region, all these exquisitely adorned crows bedecked in capes and sails or frilly hula dresses or metallic tutus are capable of performing so many different antics no one predator could truly specialize hunting a single form - save for females and unadorned subadults.

Left and below: Superb Bird of Paradise *Lophorina superb*.
Photo: Cornell University.

A superb bird-of-paradise *Lophorina superba* is a most remarkable shape shifter transforming effortlessly from unremarkable starling-sized bird into an unrecognizable object clicking, vibrating, weaving and bobbing. It is impossible that any creature treated to this performance would do anything but stare in awe.

This sort of circular reasoning that I'm submitting you to is what disciplined scientists know as "***just so stories***". New Guinea is an enormous island within islands of mountain ranges stacked atop bigger mountain ranges and jungles so tall and deep there's little hope of actually witnessing enough of the private lives of anything in the time span afforded us. A student soon learns that to conjecture for too long or rigidly about some untested idea is a folly of those allergic to hard science. I agree. Of course we can make our researches in captive settings in the traditions of Konrad Lorenz, Niko Tinbergen and Gerald Durrell. And in this long forward it is my intention to provide context for my ongoing research of the comparative psychology of gallinates, which has become quite streamlined in recent years, focusing primarily on peacock-pheasants and Pavonids. So, in the intent and purpose of returning to theoretical postulations:

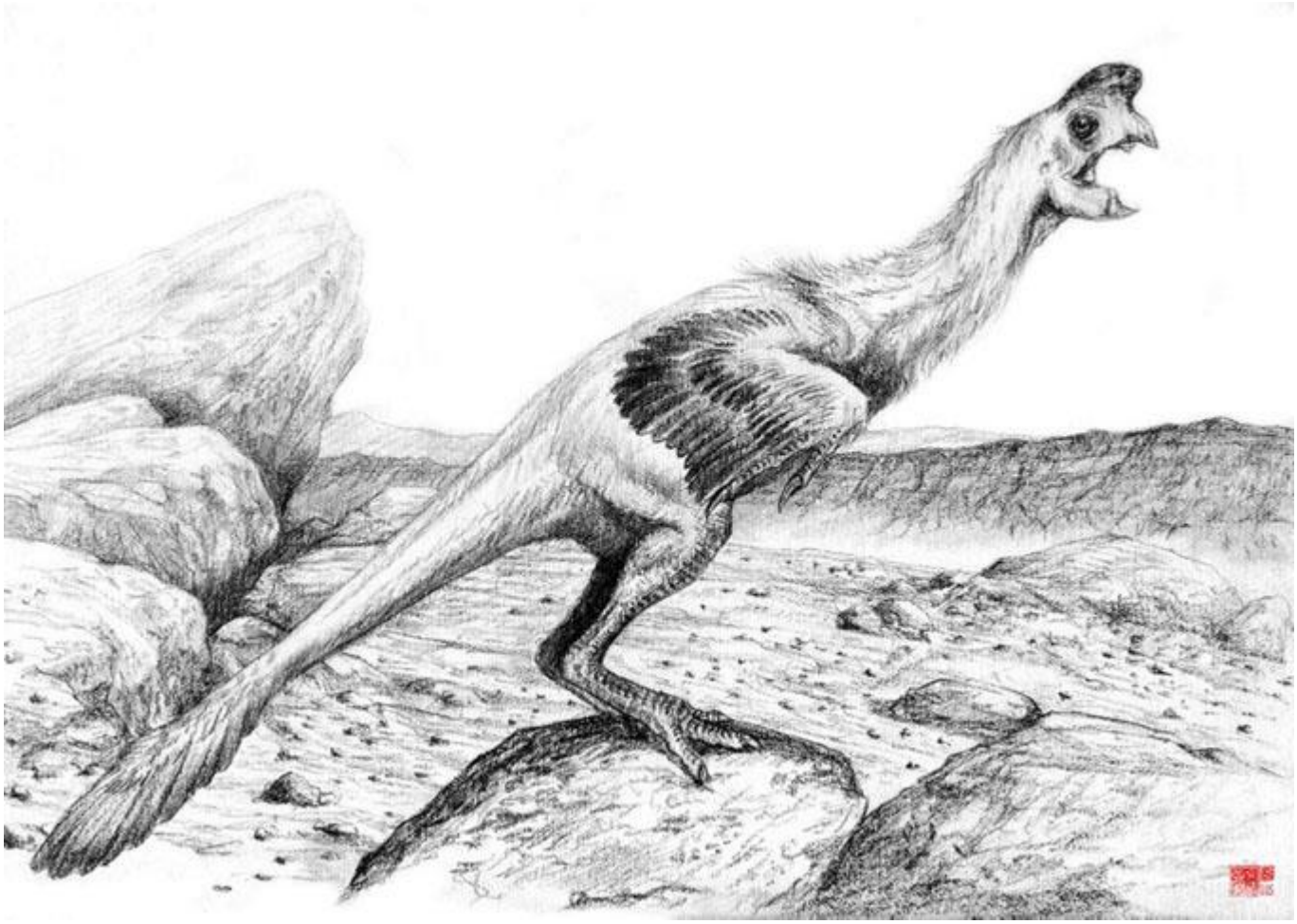
I have continually found myself challenged with questions regarding the ornamented bird. Have these exquisite and mercurially tempered creatures managed to hold their own against their oldest foes for tens of millions of years and if so how? Have the Paradisaeidae adapted some means to redirect a venomous strike to where it fails to make purchase? Are these astonishingly dazzling antics we associate with sexual reproduction effective at baffling and threatening, simultaneously broadcasting invitations to mob these most unwelcome and limbless would be predators? Does an arboreal snake need concern itself with falling to its death from the forest canopy? There are variables within variables that defy readily testable hypotheses. Nevertheless, in my opinion the perspectives of those that can only allow themselves to perceive sexual behavior in these complex adornments and behaviors have not yet engaged entirely. Parameters that frame the subject of avian evolution generally do not adequately explore questions like these. It's as if birds with "ornamental" plumage have no predators and subsist on manna from heaven. I can assert as do many that even the most exquisitely adorned birds are naturally selected sentient species with tens of millions of years of evolutionary history that has very much included predator prey and other interspecific relationships. Perhaps in birds it actually can be said that where there is form there is very likely function. It should be safe to assume the peacock-pheasant isn't bedecked in all its exquisite finery, armed with multiple kicking thorns on the backs of both legs solely to express its desire to procreate, to impress upon a female. Many ornamented bird species are so adorned/armed to insure the procreation of their species. The performances they enact before their mates are highly stereotypical pair-bonding behaviors and *most essentially*, the female's apparent disinterest is also a performance! The male's duty is to act as sentinel and distract. The female's duty is forage ably in order to produce eggs, incubate for prolonged periods with neither food nor water and subsequently brood and rear offspring, often only within earshot of the sire. Our bias is so geared toward substantiating Darwin's theories we have missed out on the most significant performance.
Reference Reference

Right: King Cobra *Ophiophagus hannah* consuming Varanid monitor lizard. Reptile saliva not only eases swallowing by lubrication, but also contains powerful enzymes to break down tissues, even egg shells and bones. But as a rule, reptiles cannot digest keratin (claws, hair, feathers) or chitin (arthropod exoskeleton). Filamentous barbules of specialized plumage become dislodged within the esophagus where they clog up the reptile's specialized swallowing apparatus. Upon ingesting an adorned bird greatly elongated and expansive feathers will extend from the reptile's throat impeding movement and rendering it more vulnerable to its own predators while digesting its prey. Consequently, reptiles learn to avoid birds with voluminous plumage.

Species with ornate feathers accentuate their weaponry with stereotypical movements and behaviors e.g., communicative signals that broadcast to would be predators that they are not only unprofitable prey, they are also noxious and potentially harmful.
Photo: Suresh Khambatta.

An Arms Race Between Reptile and Avian Theropod

Galliformes are one of the oldest surviving bird orders and any conversation on the phylogeny of these feathered dinosaurs will be well-served with a perfunctionary overview of what we do know, might know and think we might know about the earliest evolutionary history of these birds. In this instance, prepare yourself for a rather self-indulgent bottle of vintage conjecture from an unrepentant gallinateaholic. If there's a galliform involved I've probably formed an opinion about it. As you have probably determined by now, what follows will likely read as a very long digression about lots of things that have little to do directly with peacock-pheasants. Nonetheless it's critical to gain some comprehension about the *Polyplectron* from inside its psyche rather than just gazing at its beautiful visage. A peacock-pheasant is so much more than beautiful plumage and dazzling display behaviors might suggest. The significance of its evolutionary history can't be appreciated in its entirety without a refresher course on those gallinate birds that are neither pheasants nor peafowl; so archetypal that to know them is to gain a comprehension of the entire gallinaceous bird order. Perhaps this information will help us with some much-needed context.



Above: *Oviraptor philoceratops*. Sketch by Cheung.

The fossil record of Galliformes is of limited use as complete fossils of landfowl are relatively uncommon and when compared with other bird orders, data on the skeletal anatomy of extant gallinaceous species are highly limited. Over the past several decades, numerous studies have become more comprehensive. The traditional route that works with data sets of plumage and other soft tissue characters together with information on sexual behaviors and purported reproductive strategies are joined with state of the art molecular data, recombined and crunched-creating ever more robust hypothetical postulations of

relatedness amongst these birds. This has led to some really exciting advancement in our understandings on the evolutionary history of galliformes. And as is often the case, this latest research begs of us perplexing new questions. Clearly the more information compiled the more robust will be our understanding.

Modern studies agree that Australasian Megapodes, also appropriately known as incubator birds, mound builders and scrub fowl, form the first well-demarcated branch within most hypothetical phylogenetic trees of extant Galliformes. Megapodes are thusly considered basal to all remaining birds of this order. They appear to be amongst the oldest surviving landfowl, generally assumed to have emerged sometime during the Cretaceous ***over 100 million years ago***. This indicates that progenitors of these peculiar birds existed during the last heyday of the dinosaur age.

Right: Male Australian brush-turkey, (*Alectura l. lathami)* tending its mound. It could be argued that in many respects Megapodes employ a largely polyandrous reproductive system. Unlike tinamous, ratites, jacana and other incontestably polyandrus species, with males that incubate eggs and foster young to the exclusion of females until the chicks fledge, male mound builders caretake their self-constructed mounds for extended periods of time throughout the year and *within them*, (for up to 90 days) clutches of incubating eggs. The primary distinction between polyandrous bird and mound builders being that the male Megapode plays no obvious role in the rearing of its offspring.
Photo: Jenny Thynne.

Just how the earliest proto-megapode lived or what they looked like will probably remain a mystery but we can be certain they were scrappy survivors for we do know that they not only thrived in a landscape dominated by dinosaurs, (predators & competitors), they witnessed and survived the mass extinction event that obliterated most life on earth!

While we know that Megapodes are the oldest and least-derived surviving lineage of Galliformes, how their antecedents managed to survive global catastrophism is a huge unknown. But the molecular record establishes that as the Cenozoic got underway descendants of those early Megapodes diversified with major lineages maintaining their presence on respective fragments of the great landmass of Pangea. This process of the cleaving apart of landmasses through geologic ages resulted eventually in the formation and location of the separate continents identified today. Looking back at snapshots of earth history we can envision archetypal relatives of the Megapode diversifying into Cracids in southernmost South America. Soon after another great branch emerges as the earliest proto-Guineafowl radiate throughout the African continent, likewise originating from the far south.
Yet another sibling lineage colonizes Equatorial not quite yet North America, evolving into the Toothed Quails (Odontophorids). Subsequently, with the Cretaceous-Paleocene Impact Winter regenerated away via restored ecological equilibrium and the Eocene in mid-stream, Arborophilids and Pavonides emerge slowly expanding the collective geographic range of Galliformes, radiating into ecosystems that had never existed in the days of the dinosaurs and diversifying into new families. Eventually the true quail and junglefowl lineages arise from Pavonid antecedents and that was still many millions of years before the first grouse migrated with the cyclic growing and receding of Pleistocene ice sheets where they will eventually claim the Holarctic.

Before any of those marvelous families of galliform birds came into existence, when dinosaurs ruled the earth, the earliest Megapodes may have been as unadorned and unremarkable in appearance as those that exist today. They may just as likely have been as or even more elaborately plumaged as peacock-pheasants or Pavonids. I suspect that both the adorned and the unadorned existed just as they do today. Perhaps they were hunters of the parasites of dinosaurs like the modern oxpecker is to the rhinoceros or even nest predators hiding in plain sight. Regardless, those species with the most fully developed and thus insulative plumage that enabled the birds to move on wing survived the extinction event and kept on evolving.
In the absence of such a huge majority of competitors /predators perhaps the antecedents of modern Megapodes no longer required showy armaments to defend themselves and their nests. That is they may have lost them secondarily. It may be that the modern forms are descended of an unadorned and non-descript Megapode species group. There are just so many mysteries to solve in the natural universe. Even my circular reasoning allows for Occam's razor.

Above: Male Australian Brush Turkey *Alectura lathami* bullying Varanid. Note the position and elevation the lizard holds its tail. This is the most sensitive region of a reptile's body if only because the birds can pinch it within their mandibles and hammer it against the ground. The position of the brush turkey's tail signals its dominance. Note the vivid pigment glowing from the heads of both species. The Brush turkey's skin broadcasts pugilistic intentions. The blue blush of the Varanid signals that its intention is to avoid further escalation. When the brush turkey was a hatchling their relationship was very different.
Photo: Simon Leonard.

In the Absence of Dinosaurs

With the abrupt mass extinction of upwards of 70% of life on earth consequent of the **Cretaceous–Paleogene mass extinction event (K–Pg) that** marked an end to the Mesozoic Era ~ 60+ million years ago, we can be certain founding populations of modern Megapode genera were no longer faced with a great deal of their predators. The first major challenge of these archaic prototypical gallinates was undoubtedly ecological. They would have needed to be able to locate and reach places where the effect of consistent sunlight was present. It's important to keep in mind that all that ash and dust thrown into the atmosphere by the K-Pg event generated an incredibly destructive **impact winter**:

"Computer simulations suggest that the Chicxulub (astroid/meteor) impact was just the start of a devastating domino effect. The immediate force of the impact was so great it would have incinerated everything in its vicinity.

But animals and plants living on the other side of the world were not spared. Powerful earthquakes shook the planet in the hours after the impact, creating huge tsunamis. At the same time, red-hot debris from the collision rained down on Earth, igniting wildfires around the globe.

Then the impact winter set in. Dust from the collision and soot from the wildfires rose into the atmosphere, blocking sunlight. Plants had trouble getting enough light to photosynthesize, which led to a wide-scale collapse of the food web. At the same time, temperatures on the surface of the planet began to cool.
And it didn't end there. Because water holds onto heat longer than land or air, there were significant temperature differences between the atmosphere and the oceans. This gap caused large hurricanes and storms to form, churning up the seas.

This research demonstrates that one of those hypothesized kill mechanisms actually occurred -- that it got cold. That is pretty important.

The impact winter did not last long, geologically speaking. Over a period that could have lasted from a few months to a few decades (depending on location), the dust and soot fell out of the atmosphere, allowing sunlight to warm the planet once again."

- **Sean Gulick, research scientist at the University of Texas Institute of Geophysics.**
Reference

Below: Cretaceous–Paleogene mass extinction event. Illustration by Karen Kaylin.

We can envision fragmented and growing populations of a few different lineages of tropical Antarctic proto- Megapodes migrating along shore lines remaining in visual distance to open skies wherever solar radiation penetrated through the atmosphere. They migrated toward to the sun's restorative rays hastening earth's ecological equilibrium. If those Cretaceous-Paleocene prototypes of the Megapodidae were anything like the modern species, the earliest of the extent galliformes were highly precocial and yet delayed in their maturity. They were capable of long distance flights while still very young, dispersing en masse as volcanoes imploded beneath them. They went winging over open water, through typhoon winds and fog , island hopping archipelago to archipelago. Reference

Left: The monotypic, burrow-nesting species *Eulipoa wallacei* is the only Megapode to deposit its eggs nocturnally. It is also unusual for its vivid colouration, a trait not exhibited in any other species of the Megapodidae and typical for members of the Hill Partridge and Toothed Quail families. *Eulipoa* is considered the most archaic living genus of its family.
Photo: Sam Woods.

Paternal Investment

Typically, mound-builders capture the heat released from decomposition of organic materials, while burrow-nesters lay their eggs in solar or geothermally heated soils.

Megapodes are as a rule **monogamous**, some apparently paired for life, though species within the genera *Alectura* and *Aepypodius* appear to use their mounds to attract females, and while apparently socially monogamous, the brush turkeys may facultatively practice **polygynandry** where two or more females associate with and breed with two or more males. This borders on promiscuity but is apparently limited to a discrete number of potential mates, which are enforced primarily by resident females that pursue strange females from their home ranges, which tend to be substantial in area It can be said however that by and large most species of Megapodes are to be found singly or in solitary pairs. They remain in regular vocal contact with one another as well as their neighbors year-round. Some species communicate via subsonic booms that can be felt/heard for considerable distances.

Left: Nesting colony of the burrow-nesting Maleo *Macrocephalon maleo* Megapodes that deposit their eggs 'in volcanic soils relying on solar heat or geothermal energy for incubation' abandon them shortly thereafter, providing no additional care. These species tend to also nest somewhat communally possibly because of the relative scarcity of optimal nesting sites.
Photo: Martín Cagliani.

Perhaps most intriguingly, many Megapode species are known for the habit of incubating their eggs in 'homeothermic' mounds composed of decaying vegetation and earth constructed and maintained by the parents.

Obviously it requires a considerable expenditure of labour to construct a mound and that responsibility is primarily that of the male, which is also obliged to defend it from interlopers that may attempt to usurp it. Males control temperature and humidity with incredible proficiency. Most species service their mounds year round, though once constructed to a specific phase, maintenance can be quite minimal.
Larger, more established mounds might be left for a few days at a time allowing males more opportunity to search for food. Males of at least one species of the genus *Megapodius* build fresh mounds upon older ones, creating imposing structures of enormous circumference and height.

Left: Hatchling *Macrocephalon maleo*. There are indications that Megapode chicks are sociable with one another and become so without previous conditioning or imprinting so common in other gallinates. Photo: Pat Markle.

Within two weeks Megapode chicks remain in vocal distance from one another at all times. Compared with some other gallinates, extent Megapodes are not particularly exciting to look at given the monochromatic tones of their plumage. Nonetheless, they are amongst the most fascinating of birds in that they do not incubate their eggs with their own body heat nor do they brood their chicks. Hatchlings emerge from beneath leaf litter or sand, from 49 to 90 days to embark on lives apparently independent of their parents. Ecological parameters of their natural habitats make this possible as they live as a rule at latitudes very near the equator where temperatures are constant and daylight hours hardly differ from one month to the next. Further, the highly sedentary adults' perpetual raking of substrate may improve upon foraging quality of the forest floor.

Above: Giant Gippsland Earthworm *Megascolides australis* and Giant Blue Earthworm *Terriswalkeris terraereginae* and other archaic anthropods are optimal foods for Megapodes. Their flesh contains complete amino acids and their chitin provides an excellent source of starch e.g. readily procurable energy, a great necessity for the birds as they move immense amounts of substrate, construct and maintain their nesting sites in immense humidity and heat. Like some Cracids and Neotropical Odontids, Megapodes use their feet to subjugate prey and manipulate plant matter. Megapodes are particularly fond of decaying fruit but their most important foods appear to be starchy roots, drupes and terrestrial crabs, slugs, snails, ants, and any other small animals they uncover scratching and digging in the forest floor. They are one of the few creatures that regularly consume millipedes, which tend to be noxious to most animals.

Logically, in the process of mound building and maintenance activities males uncover quite a lot of nourishment. Some anecdotal accounts of indigenous people, report that Megapodes keep these mounds year round to farm their own bird gardens. As the Megapode egg yolk is ~ 50-70% of the egg's weight and clutches quite large (up to 20+), females are obliged to forage afar to insure adequate ingestion of optimal nutrients required to produce viable embryos.

Left: Pair of Australian Brush Turkey *Alectura lathami* engaged in egg deposition. The initial act of egg deposition is intriguing in of itself. The males excavate a number of pits for the females to inspect and select from within which they will deposit one egg every few days. Males of some species will typically harry females around the mound eliciting obligatory pair-bonding postural display behaviors; a pair ritualistically performs before the male is receptive to the female's trade off. The male stands beside its mate carefully inspecting the laying of the egg. The length of incubation of a Megapode egg may be up to 90 days during which time the male dutifully attends to the incubation mound, maintaining ideal temperature and humidity levels throughout the year. We can probably infer that males make attempts to safeguard that the eggs deposited within its mound are exclusively its own. Photo: Eric Lindgren.

As the chicks emerge from their mounds ready to fly, requiring no further parental assistance, we can be assured that the nutritive value of egg yolks which nourished their embryos are exceptionally high and as such, a successful hatching is an indication of optimal ecological conditions that enable females to forage consistently on optimal nutrition and proficient male incubation/ guardianship.

Right: Australian Brush turkey pair harassing monitor lizard they've encountered within their foraging territory. Varanids are a constant menace, digging into mounds in search of eggs and hatchlings. But despite these great lizards' size and temperament they are reluctant to engage for the Megapode's tenacious pugnacity. While it is difficult for the birds to protect every egg, they are capable guardians. The Megapode's habit of producing large clutches (up to 25 eggs in some species) and burying them deep within the soil has been an effective strategy of reproduction for many millions of years. Photo: Simon Leonard.

Close Combat

Regardless of how uncannily proficient their incubation mounds may be, reproductive strategies of Megapodes have their shortcomings so far as predators are concerned. This is one of those unambiguous truths zoogeography reveals. As a rule, Megapodes are absent

from regions that host many placental mammalian predators. The only native mammalian predators of New Guinea and Australia are marsupial and even then not particularly high in number. Marsupial predators like opossums are far from harmless but clearly not as mentally complex or capable as placental mammals. One of the primary predators of Megapode nests is the Varanid, those curiously intelligent carnivorous quadrupeds known as monitor lizards/goannas.

Megapode eggs are immediately buried upon laying and this may help to conceal any telltale odors that could attract Varanids. Likewise, upon their hatching, Megapode chicks are obliged to burrow out of the mounds. In doing so they are thoroughly cleansing their pelt-like natal plumage of any telltale scent remaining from its egg. This is critically significant given that Varanids are capable of detecting food from surprising distance and are indefatigable nest predators.
Male Megapodes are infamously territorial, pursuing and assaulting animals that intrude upon their mounds. But the monitor lizard is evolutionarily brilliant and hence incredibly persistent. Many Varanids rest high in trees that afford them olfactorily and visually strategic vantage points. They detect potential food larders, (nests and carrion are favorites), not only by smell/taste but also by sight. Even though these great lizards are attracted to the commotion of Megapodes tending their mounds, eggs are not present year round and male Megapodes are irksome and dangerous. It is likely that individual monitor lizards learn early in their lives that it is not energy efficient or safe to visit any one mound for long.

It may well be that the Megapode's best defense is its offensive strategy. Not only does it persistently draw attention to itself maintaining and building upon its mound throughout the year, the male also defends its territory aggressively; engaging any and all potential (ectothermic) egg thieves by nipping at the most sensitive extremities, e.g. the tail tip and toes, provoking the reptile to strike and repeatedly. The lunging of the agitated reptile's strike is anticipated by the bird, which orients itself in such a manner that it remains positioned with the widest surface area of its body, i.e., the expanded wing and tail closest to the reptile, versus the vulnerable breast maintaining a distance just a smidge past striking range. The bouts of close combat where bird and reptile actually fight with beak, fangs, wings, claws and whipping tails are fairly brief. The Varanid (or python) is generally somewhat fixed in place, on defense against the feathered dinosaur. The male Megapode remains in perpetual motion, keeping the reptile preoccupied by running and pacing in concentric circles; nipping, dodging, laterally positioning itself like a matador torturing a bull. It is very often the case that an agitated ectothermic intruder will become overheated in the encounter and exhausted its flight impulse is engaged and it moves off elsewhere. Of course when the reptile is finally in retreat mode the male Megapode is at its fiercest, assaulting the intruder with an escalation in intensity. Try to keep in mind how much smaller birds including Passerines and Woodpeckers are just as fearless in their contempt for snakes far larger in direct proportion. Reference

Right: Day-old hatchling Tabon Megapode, *Megapodius cumingii*. Megapodes are capable of making sustained flights over prolonged distances within only a few months of age. It is at their juvenile developmental phase that these birds appear to disperse by wing, often reaching what will be their new home ranges via archipelago hopping.
This phenomenon is likely responsible for diversification within the species and an adaptation of life on actively volcanic islands. Photo: Pamela Rasmussen.

Above: Malayan Great Argus *Argusianus argus.*
The argus is well-armed with serpentine patterned shields and distracting false limbs that make its matador dance against large reptilian foes all the more exhausting for their opponents. The Pavonid is so perfectly adapted for this fight- even the varanid's worst predator the python soon learns to avoid attracting the attention of this obsessive pugilist. Just as males of mound building Megapodes are highly sedentary and territorial over their constructions; males of their distant cousin the Great Argus create large clearings within the forest, which they keep fastidiously clean for most of the year. This is no small effort given the immensity of the great primary forest trees all around them and frequency of rain torrents washing their canopies. No leaf or twig, drupe, amphibian, centipede, moth or ant will remain within that arena for long. It's either carried off and deposited in the peripheries or consumed there on the arena. And just as the Megapode often wages battles with giant lizards and pythons, so too does the great argus. The progenitors of this archetypal Pavonid have been locked in a battle of wills with the monitor lizard and python at least since the Eocene some 50 million years ago.
Photo: Khizer Umarji.

While these peculiar birds of the family Megapodidae are almost entirely absent from the native haunts of advanced mammalian predators like felines and civets, all but those species that inhabit the most remote islands of Oceania certainly do cohabitate with Varanids as well as serpents, which prey heavily on eggs and chicks. Megapodes inhabit regions where the python has been present since at the least the Oligocene ~ 40 million years ago, though it is believed that this class of predator did not arrive in the Australasian bioregion until ~ 20 million years after modern Megapodes had emerged there. Still more compellingly, according to (Vidal et al) Varanids are strictly Asiatic in origin and did not arrive in the Australasian biogeographic region until sometime during the Mid-Miocene, ~ 15 million years ago. This suggests that Megapodes adapted to predation pressures imposed by serpents for ~ 5 million years before they were exposed to this second class of even more ecologically intelligent and predatory reptile, which unlike snakes need to eat regularly and are capable of digging and climbing with four limbs. When Varanids finally reached in New Guinea/Australia they probably exploited niches largely unoccupied or frequented by less formidable species. As the Australasian biogeographic region appears to be the centre of distribution of post Impact Winter Megapodes, the antecedents of modern species existed for a significant portion of their evolutionary history without Varanids

digging up their eggs. It's telling that molecular diversification of the different Megapode genera appears to have taken place largely during the Miocene when Varanids appeared. Perhaps the sudden re-acquaintance with a class of predators they had not had many dealings with since Cretaceous times kick-started Megapode speciation.

Above: Malleefowl Leipoa ocellata engaged in pair bonding display ritual. In confrontation with reptilian intruders the birds utilise very similar postures and behaviors.
Photo: **Camera trap Malleefowl conservation farm.**

As the Australian continent has become increasingly arid since the Miocene, the subtropical jungle adapted ancestors of the malleefowl *Leipoa ocellata* adapted with each ecological phase. They witnessed and survived the decline of the rainforest and the emergence and eventual domination of acacia scrub and eucalyptus. The malleefowl is apparently the only species of Megapode adapted for life in semi-desert environments.

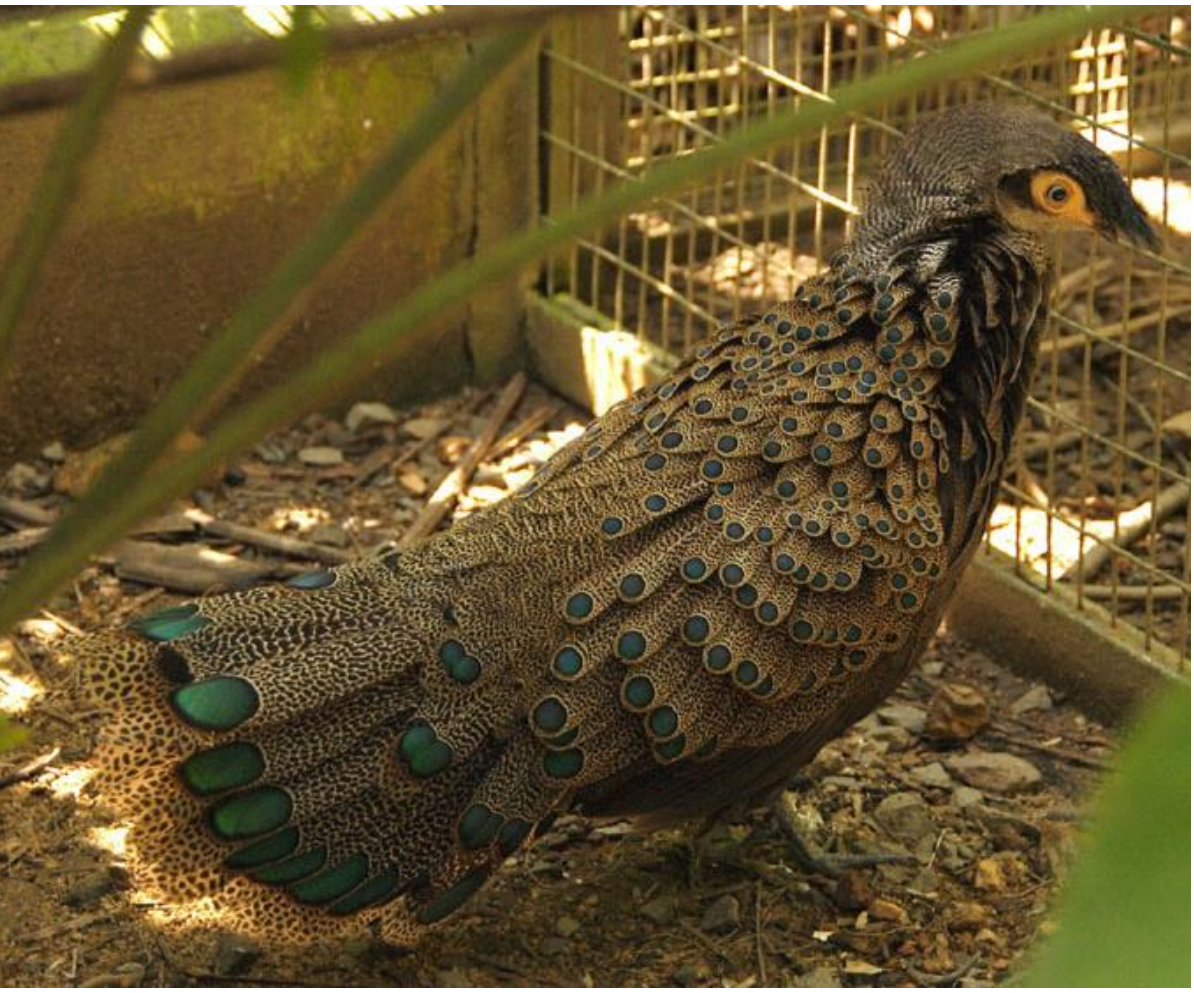
What is perhaps most immediately compelling about *Leipoa* is its exquisite plumage. It's the only Megapode that exhibits such complex and intricate markings.
Environmental and predatory challenges have resulted in the malleefowl's remarkably cryptic plumage. This may have arisen via natural selection by the class of (native) predators most likely to take adult birds. At least two species of eagles are known to prey upon fully mature malleefowl.

Right:
Scrub fowl leaf litter mound. Varanids prize eggs above most food items because they provide a complete source of nutrition including fat, vitamins, complete amino acids, calcium and water.
Photo: Jackson Helms.

Above: The malleefowl's contour plumage is bedecked with striking markings analogous with ocelli exhibited in other gallinates. The mantle, scapulars and entire wing are patterned in constellations of these bold patterns. This is of particular interest, for the malleefowl's markings cover its body in precisely the same manner as those of the peacock-pheasant. Photo: Magnus Manske.

Below: Female Annamese Peacock-Pheasant *Polyplectron germaini.*
Protective colouration and patterning of peacock-pheasants make it challenging for a reptile to assuage where to strike with precision. Photo: Charles van de Kerkhof.

While both classes of reptilian predators inhabit the malleefowl's scrubland habitat, relatively few creatures thrive there. Consequently, from a behavioral ecology perspective interspecific communications between malleefowl and ectotherm are particulary fascinating. When its general vicinity has been intruded upon by a reptilian predator, for example in those instances while the malleefowl are foraging within their home territory and happen to discover the presence of some desert python it contradicts all the laws of crypsis. This is when the malleefowl shape-shifts, making itself appear larger and suddenly highly visible. Demanding full attention, the malleefowl repeats the basic anti-predatory sequences as described in accounts of the brush turkey, but whereas the former keeps itself laterally oriented to the head of the reptile, rectrices held at their greatest height and width; the malleefowl employs a different method to displace its foe. It approaches with wings spread nearly to their greatest capacity. It lunges forward bowing with breast restrained, bill straining downward as if into the throat at a degree reminiscent of that of a peacock in its attenuated radiating posture. The malleefowl dances rhythmically alternately expanding and retracting its wings as it raises the terminal ends of robust secondary wing quills, revealing tertials, scapulars and wing coverts prominently adorned in splendid warning patterns. While in motion these specialized markings make the malleefowl's feathered shields all the more effective as their activity and position conceal vulnerable regions of the bird's body. This is critical for if the reptile is able to puncture muscle with its fangs all bets are off and the bird may very well end up on the losing badly. Dizzying stars make it difficult for a reptile to track the birds undercarriage effectively. This suite of highly ritualized and stereotypical anti-predatory behaviors elicited by a specific class of predators (reptilian) is important to keep in mind when we get to discussing nest defense strategies of peacock-pheasants. While it's been accepted as a matter of irrefutable fact since Darwin's manifesto, that males of those most sumptuously plumaged of birds have no investment in the perpetuation of their species beyond copulation, we only need observe nest defense behaviors employed by other gallinates, like the malleefowl. In exploring the comparative psychology of these birds we may throw light on the evolutionary convergence of peacock-pheasants and Pavonids.



Left: Adult male Malayan peacock-pheasant *Polyplectron malacense* with rectrices and tail partially elevated, neck plumage erected, ephemeral ruff expanded and forecrest extended forward. This combination of physical cues is utilized in recognition displays between members of the same species as well as during preliminary anterior threat displays with interspecifics.

Right: A female Yellow-Knobbed Curassow *Crax daubentoni.* Unlike most Galliform families, the Cracididae have evolved in a hemisphere that hosts no Varanids nor other large predatory lizards. Photo: Kevin Burkett.

Left: Dusky Megapode *Megapodius freycinet*. Few gallinates are capable or at least willing to fly over large bodies of water. Megapodes inhabit many remote islands. Compellingly, it is at the juvenile developmental phase that Megapodes disperse. Species of the island-adapted scrubfowl of the *Megapodius* genus do not exhibit striking colours, markings, or patterns in their plumage. They are as a rule the colour of volcanic ash, forest hummus and clay.
Photo: Hanom Bashari.

Left: Male Common Grey Peacock-Pheasant *Polyplectron bicalcaratum* performing anterior threat display to caged serpent within behavioral research enclosure. Male gallinates that act as sentinels over nesting sites utilise a whole repertoire of postures, vocalizations and behavioral cues that broadcast information about environmental conditions, including the approach and/or presence of potential threats. The birds keep up a lively conversation with other members of their species easily eavesdropped upon by cohabitant species the first phase of most defense behaviors develop silently, ,from stationary alert posture. This enables the birds to not only detect a threat without revealing their own locations, but also enables them to identify the intruder and take appropriate action.
Photo: Kermit Blackwood.

Below: Bengal monitor *Varanus bengalensis* and Sri Lanka peafowl *Pavo cristatus singhalensis* engaged in preliminary stages of a typical interspecific encounter between bird and reptile, whereby individuals of two different species communicate via stereotyped behaviors that advertise temperament, weaponry and intention. These exchanges have no winners or losers. The objective appears to be conflict avoidance and/or conflict resolution. Exploring interspecific territorial defenses may help us gain more understanding about the evolutionary history of peacock-pheasants and gallinate birds on the whole. Photo: Kerry Thomas.

Megapodes, Cracids, Odonts, Numids and Arborophilids are generally monogamous, even permanently so. Males are guardians and custodians of nest sites and progeny. They actively patrol their home territories, excluding any intruding reptiles they encounter. The distinction between male Megapode building a giant homeothermic incubation mound and the Arborophilid constructing knitted shanty mound nests isn't narrow, but clearly there are similarities between the two reproductive strategies.

Left: Adult female Red-billed Hill-Partridge *Arborophila rubrirostris*. Arborophilids may migrate in elevation from forest floor to subcanopy during the wet season. Photo: James Eaton.

Right: Adult Male and juvenile dark-backed wood-quail *Odontophorus melanonotus* and other Odonts are derived of an archetypal gallinate ancestor phylogenetically intermediate between Megapodes and Cracids. Photo: Larry Thompson.

Left: Adult male Roul Roul Wood-Partridge *Rollulus rouloul* and other Arborophilids are derived of an archetypal ancestor phylogenetically intermediate between Megapodes and Numids. Photo: Myron Tay.

Below: Female *Rollulus roulroul* (note vibrissae forecrest). Roul roul are sexually dimorphic yet monogamous and facultatively socially polyandrous, as is the case with *Guttera* and *Phasidus* guineafowl and *Ithaginis* tetraophasinids. Photo: Vicki Milway.

Below: Wood Partridge and other Arborophilids construct shanty mound nests from leaf litter and mosses, within which they incubate their eggs while partially buried. Several male Roul Roul may participate in its construction, cooperating with the mated pair by carrying nesting material and acting as sentinels over the nest mounds. Several families of Roul Roul will crèche their chicks in a manner reminiscent of the *Guttera* guineafowl. Several unmated males generally employ themselves as crèche guardians (headmasters), frequently advertising their "reciprocal altruism" to breeding pairs in the process. Photo: Peter Stubbs.

These oldest and most basal of Galliformes, each and every genera within their respective families: Megapodes and Cracids, Odontophorids, Numidids and Arborophilids are generally monogamous. Pairs may remain together indefinitely. And from my experience peacock-pheasants are likewise, more or less strictly monogamous, though there is evidently some threshold for social polyandry in some species which I will cover later. When allowed to self-select for mates and reproduce naturally, the same peacock-pheasant pairs remain bonded year after year. Potential nesting sites are discovered by males, which generally alter them slightly before inviting their mate to inspect. It will carry nesting material from time to time and sometimes rearrange the peripheries of the nest when inspecting its eggs. Once the female has gone to setting, the male guards over its nesting territory rather fearlessly. It becomes more sedentary, rarely if ever moving beyond hearing distance of the nest. Males of the ornate species maintain clearings in strategic locations within their home ranges, which they occupy for extended periods of the year. They create berms fashioned from excavated soil situated near the centre of their clearings.

In this curious behavior exercised only by the least-derived and primitive *Polyplectron* species, it's impossible not to wonder if the male peacock-pheasant's scrape and pitching mound is not analogous with the earthen incubation mound of the Megapode and leaf litter shanty mounds of Arborophilid and Odontophorids.

Though the opposite has been maintained by some authors, in my own experience I have never known a single species of peacock-pheasant where the male of a pair, if given the opportunity to do so, played no part in nest selection, nest defense or chick rearing. In a captive situation this requires some special preplanning for the males tend to harry females and even the chicks if appropriate targets for their frenetic energies are not provided. In the next installation of this short series, I will discuss the natural history of each of the different peacock-species as well as introduce the little-known Asiatic spurfowl of the genus *Galloperdix* and the crimson-headed wood-partridge *Haematortyx,* which are very likely the peacock-pheasant's closest living relatives and which may link the *Polyplectron* with Arborophilids. If either of these affinities proves to be correct, the phylogenetic position of peacock-pheasants is well outside that of either Pavonides or Phasinids.

Left: Palawan peacock-pheasant male *Polyplectron emphanum* on nest incubating eggs.
Photo: Monte Nazelrod.

In the next installation of this essay we will explore the biology and natural history of Galloperdix and Haematortyx e.g. the Asiatic spurfowl, together with a corresponding overview of each of the different Polyplectron species.

Acknowledgements: Thank you for generous assistance and consultation from Darren Naish (UK) and Dan Wharton (USA) and each and every photographer whose work is represented here: Charles van de Kerkhof, Cheung, Cornell University, Denise Menias, Eric Lindgren, Hanom Bashari, Jackson Helms, James Eaton, Jenny Thynne, Karen Kaylin, Kerry Thomas, Kevin Burkett, Khizer Umarji, Larry Thompson, Magnus Manske, Mark Vaughn, Martín Cagliani, Monte Nazelrod, Myron Tay, Pamella Rasmussen, Pat Markle, Peter Stubbs, Sam Woods, Simon Leonard, Suresh Khambatta, Tomasz Doron, Vicki Milway. Also thank you to Tom Blendulf, Christine Sheppard and Don Bruning, Frank Lin, Ross Dupuis, Gareth Dyke, William Stein, George Barrowclough and Rebecca Kimball.

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Photo: Roul Roul hen with keat.