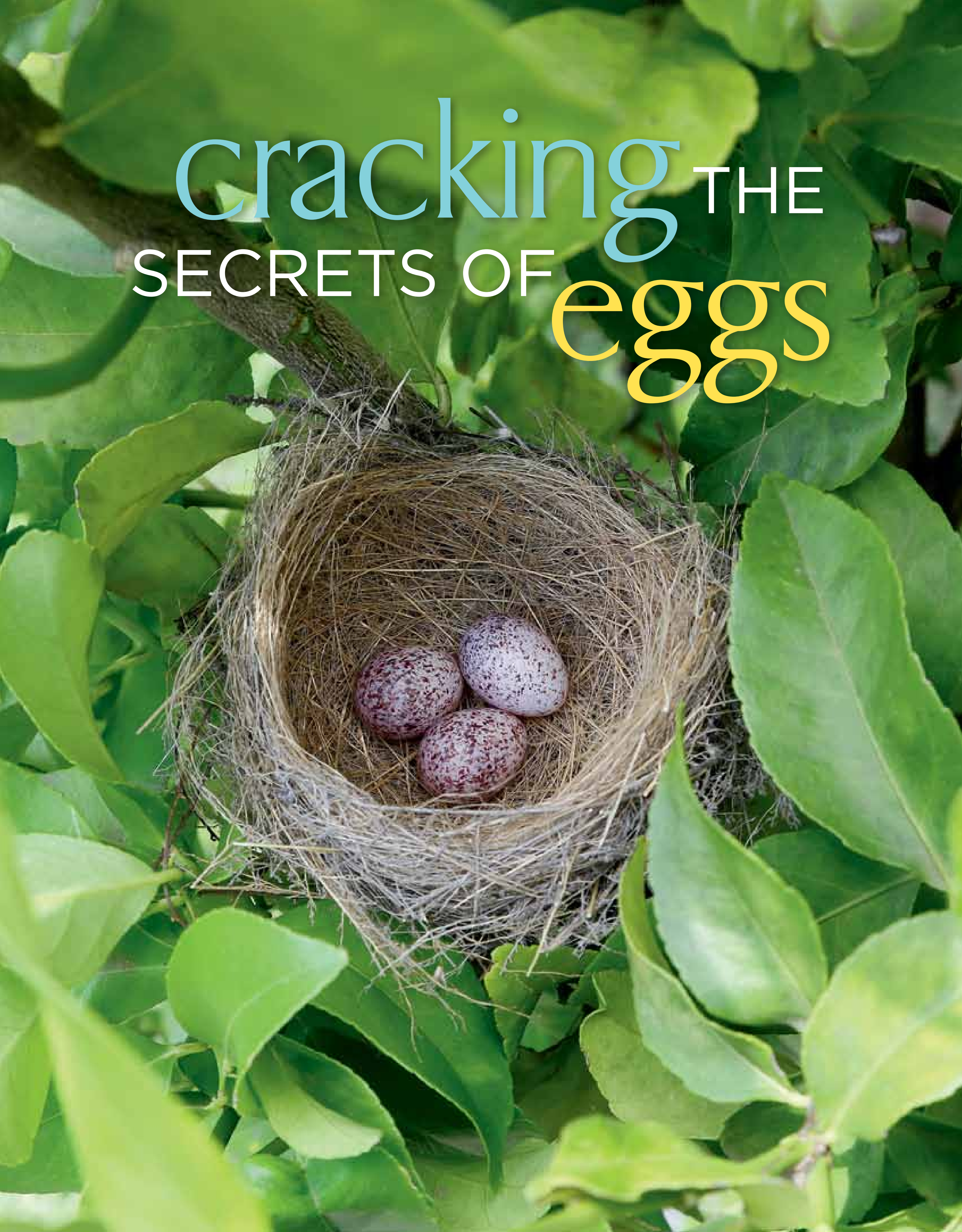

cracking THE SECRETS OF eggs

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PHOTOGRAPHS **WARWICK TARBOTON**

ALL BIRDS LAY EGGS. These four words, seemingly trite, in reality describe a puzzling biological phenomenon. To appreciate why, consider reproduction in the two groups of animals most closely related to birds: mammals and reptiles.

Among mammals, reproduction can involve egg-laying (echidnas and the platypus) or live birth (all other mammals). Similarly, reproduction in reptiles can involve egg-laying, live birth preceded by the incubation and hatching of eggs within the mother's body, or even live birth after embryos develop in a manner remarkably similar to that of most mammals. A similarly diverse spectrum of reproductive strategies exists in most other animal groups.

So the ubiquity of egg-laying in birds represents an exception rather than the rule. But why has live birth never evolved in birds? The implications of the extra weight on flight ability may be one part of the answer: lugging around an increasingly heavy load as young develop internally would severely impact manoeuvrability. Another factor may involve temperature. Avian embryos, like those of mammals, need to be at 36 to 39 degrees Celsius for normal development, and higher temperatures can be lethal. Avian body temperatures are typically above 40 degrees, and so may inherently be incompatible with embryos developing within the mother's body. The fact that most birds have higher body temperatures than mammals is probably related to the intense muscle activity required for powered flight.

What is an egg?

An egg, essentially, is a survival capsule for the developing embryo. As the embryo develops from a single fertilised cell into a fully formed hatchling, its requirements are much the same as those of any adult bird: a supply of oxygen, water and nutrients, and a way to dispose of carbon dioxide and waste products.

The yolk, which consists primarily of proteins and fats, provides nutrition for the embryo. It also contains antibodies produced by the mother's immune system, which kick-start the developing immune system of the embryo and provide it with defences against pathogens. A little-known fact is that not all birds' eggs have yellow yolk; that of the Lesser Black-backed Gull *Larus fuscus*, for example, is bright red.

The albumen (egg white) surrounds the embryo and the yolk and serves as a source of water and a shock absorber, as well as a thermal buffer against sudden changes in temperature. Waste materials produced by the embryo are handled by a structure called the allantoic sac, while the uptake of oxygen and release of carbon dioxide occur through thousands of microscopic pores in the shell. The shell, of course, provides physical protection to the egg, and is often pigmented in such a way as to be camouflaged.

All shapes and sizes

Relative to the birds that lay them, eggs range from being tiny to eye-bulgingly huge. In general, the smaller the bird, the larger the egg as a percentage of adult body mass, but there is often considerable variation among similarly-sized species. Relatively large-egged groups include the Procellariformes (the albatrosses, petrels and allies) and Charadriformes (the waders and gulls). The small-egged end of the continuum consists of groups like the Columbiformes (doves and pigeons) and Cuculiformes (cuckoos, coucals and allies).

The largest egg laid by an extant bird is, of course, that of the Common Ostrich *Struthio camelus*, but each ostrich egg represents just two or three per cent of the mother's body mass. On the other hand, spare a thought for the female Brown Kiwi *Apteryx australis*, whose single egg can represent a staggering 20 per cent (one-fifth) of her body mass. To put this into context, a Brown Kiwi is approximately the same size as a chicken, yet her egg weighs about the same as seven chicken eggs. The fact that kiwis have such massive eggs is thought to reflect their evolutionary descent from moa-sized ancestors with moa-sized eggs; essentially, kiwis shrank faster than their eggs. This mismatch probably arose because benefits associated with large eggs resulted in weaker evolutionary pressure on egg size compared to body size. >

above *Extremes of egg size among southern African birds. Shown to scale.*

opposite *Birds are unusual among vertebrates in being exclusively egg-laying. These are the eggs of a Dark-capped Bulbul.*

GREAT WHITE PELICAN

KNYSNA TURACO

WATTLED PLOVER

above *The shapes of eggs vary considerably, from nearly spherical to sharply pointed.*

above, right *Incubation in Yellow-billed Ducks is uniparental, with the female incubating the eggs for about four weeks.*

Eggs also vary considerably in shape. The eggs of owls and turacos are almost spherical, whereas those of many shorebirds are much more sharply pointed at one end than the familiar shape of the chicken egg. Part of this variation is related to the nest site: spherical eggs are common in hole-nesters, but species that nest on cliffs and other sites where eggs could easily roll out often have sharply pointed eggs to reduce the likelihood of this happening. Other explanations have focused on how shape influences the way eggs fit into the space under an incubating adult. Recent models suggest that spherical eggs provide the optimal use of space in species that lay single eggs, symmetrically oval ('biconical') eggs are ideal when the clutch size is two or three, pointed eggs are best for clutches of four to seven, and in clutches larger than seven, eggs should again be spherical.

Keep 'em warm...

The eggs of most birds are laid in locations where temperatures are significantly cooler than the optimal range for embryonic development. With a few interesting exceptions, the heat needed to maintain the temperature of the eggs above that of the environment is provided by one or both parents, forming the basis for one of the most quintessential of avian behaviours: contact incubation.

The relative roles of the adults during incubation vary: in approximately half of all taxonomic families incubation is shared by both parents, while female-only incubation occurs in around 40 per cent and male-only incubation in around six per cent.

While incubating, an adult needs to produce enough body heat to maintain its own temperature plus warm the clutch of eggs underneath, often for extended periods. The efficiency of heat transfer to eggs is often enhanced by the presence of one or more brood patches, areas of bare skin in close contact with the eggs, and in some species by vascularised feet. During this time, the adult cannot obtain food or water (unless of course its mate feeds it) and is often vulnerable to predation. Should the incubating adult leave the nest, the eggs immediately start cooling and there is the risk of their temperature dropping below the range required for embryonic development.

During the evolutionary history of birds, incubation behaviour has been shaped by a fundamental trade-off: time on the nest is good for the eggs but potentially bad for the adult, whereas time off the nest is bad for the eggs, with cooling leading to slower development.

IN APPROXIMATELY HALF OF ALL TAXONOMIC FAMILIES INCUBATION IS SHARED BY BOTH PARENTS, WHILE FEMALE-ONLY INCUBATION OCCURS IN AROUND 40 PER CENT AND MALE-ONLY INCUBATION IN AROUND SIX PER CENT

Delayed development also increases the period between laying and hatching, which can be bad news for eggs as well as parents if predation risk is high. Nest attentiveness during incubation varies, with an adult being on the eggs virtually continuously throughout the incubation period in groups such as penguins, doves and nightjars. In others, including swifts and many passerines, eggs spend an average of 25–30 per cent (and in some cases more than half) of their time unattended.

The demands and trade-offs imposed on incubating adults are nicely illustrated by Joe Williams' study of Orange-breasted Sunbirds *Anthobaphes violacea* in the 1990s. The female incubates the two-egg clutch alone for approximately a fortnight during the winter months, when rain is a regular occurrence. During the day, each incubation bout lasts in general 12 minutes, with periods off the eggs averaging about eight minutes each. The female thus spends about 40 minutes of each hour incubating and around 20 minutes foraging. The time the female spends off the nest increases towards sunset, when she puts in extra foraging effort in preparation for her overnight fast.

The result of the time invested by the female sunbird in incubation behaviour is an overall average egg temperature of slightly below 35 degrees Celsius, reflecting the fact that the eggs cool below the optimal range whenever she is off the nest. Sometimes egg temperature drops far below the range required for embryo development; females occasionally remain off the nest for long periods during heavy rain in the late afternoon, and in these instances the eggs can cool to near 10 degrees Celsius.

One of the most significant contributions of Williams' study was that he quantified the energy used by the sunbirds while incubating. His data revealed that incubating females work extremely hard, and in fact they maintain rates of energy expenditure that exceed by a substantial margin the maximum values predicted by some theoretical models. In the paper reporting his findings, Williams noted that it is difficult to imagine birds working any harder.

The only birds in which incubation occurs entirely without heat transfer from an adult are the megapodes, the Australasian brush-turkeys and scrubfowls. Most >

A male African Jacana, here showing the species' characteristic behaviour of holding eggs against his brood patch with his wings, bears sole responsibility for incubation.

above *Many ground-nesters, including this Double-banded Courser, lay and incubate their eggs in exposed locations.*

right *Laughing Dove eggs on the simple stick platform nest typical of this group of birds.*

opposite, top *Incubating in the furnace… A Sclater's Lark on its nest on the gravel plains of the Nama Karoo.*

megapodes bury their eggs under massive mounds (up to 4.5 metres high, in some cases) of rotting vegetation, and the heat produced by microbial decomposition keeps the eggs at a suitable temperature. Despite being freed from the rigours of incubation, megapodes are nonetheless dutiful parents and continually add or remove vegetation to fine-tune the temperature inside the mound.

Some species lay eggs in tunnels that are heated by the sun, or even geothermal heat. An intriguing and superficially similar incubation strategy has been documented in the Crab Plover *Dromas ardeola*, a species completely unrelated to megapodes. This species breeds colonially on beaches in the north-west Indian Ocean, and excavates burrows around three metres long and usually slightly more than half a metre below the surface. The female then lays a single egg in the tunnel, placing it about halfway along the tunnel's length. After laying, the adults spend very little time incubating, with the egg sometimes being left unattended for a day or more at a time. But because of the intense daytime solar

radiation at the surface, together with the thermal inertia of the sand, temperatures in the burrow remain in the mid-30s around the clock. So while outside temperatures range from scorching by day to frigid by night, the site where the egg is laid remains within a degree or two of the optimal temperature for embryo development.

Keep 'em cool…

For the majority of birds, the incubation period is a struggle to keep eggs warm. But for birds breeding in extremely hot habitats, the challenge is often keeping eggs cool enough to avoid lethal hyperthermia. In North America's intensely hot Sonoran Desert, for example, during the height of summer when air temperatures are in the mid-40s, incubating White-winged Doves *Zenaida asiatica* offload heat to the environment so rapidly that their body temperature drops a degree or so below normal levels. The purpose of this seemingly paradoxical phenomenon is to facilitate the transfer of heat from the eggs to the adult so that it can be dissipated by way of evaporation.

Many birds that nest in hot, arid environments face a conundrum. From a thermal perspective, the best place to nest is in any available shade, perhaps at the base of a scraggly shrub. The problem is that nesting in shady spots also makes eggs and chicks more vulnerable to predators like mongooses, which tend to keep near cover while doing their rounds in search of prey. This seems to be the main reason why some birds lay their eggs in seemingly bizarre locations where they bear the full brunt of searing temperatures.

A prime example of a bird that nests in exposed sites is Sclater's Lark *Spizocorys sclateri*. This species lays its single egg in a cup-shaped hollow scraped by the adult on the gravel plains of the Nama Karoo, where intense solar radiation combined with sweltering air temperatures make for some of the most inhospitable breeding conditions imaginable. Observations by Penn Lloyd in the 1990s revealed how this species manages to breed under these conditions. Teamwork is critical: the parents alternate incubation duties, with shifts sometimes being as short as 10 minutes. The larks nest near water sources, so they can drink frequently and avoid becoming dehydrated despite near-continuous panting while on the nest.

Other species that nest in searing environments, most notably shorebirds, rely heavily on belly-soaking behaviour. Many plovers, for example, cool their eggs by visiting water and soaking their belly feathers before returning to incubate. One of the most potentially interesting but currently under-studied groups in this regard is the nightjars. Adults of some species incubate eggs throughout the day in exposed, sunlit locations without any water intake, belly-soaking or other thermal relief. Under these conditions severe dehydration seems inevitable, and the physiological processes that permit these birds to survive remain unclear. ◆

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RED-CRESTED KORHAAN

GREAT SPOTTED CUCKOO

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