A common feature of modern birds is the absence of the heavy skulls and enamelled teeth found in their predatory reptilian ancestors. In this article, Phil Hockey explains why this happened and explores the evolutionary doors that were opened to birds as a result.

More than 150 million years ago, when the Earth rumbled to the tread of the ruling archosaurs, a novel adaptation was slowly being added to the tapestry of evolution. In time, this adaptation was to have a profound impact on the diversity of life on the planet, and would also provide the explanation as to why one particular group of dinosaurs was able to survive the massive Cretaceous–Tertiary extinction of 65 million years ago.

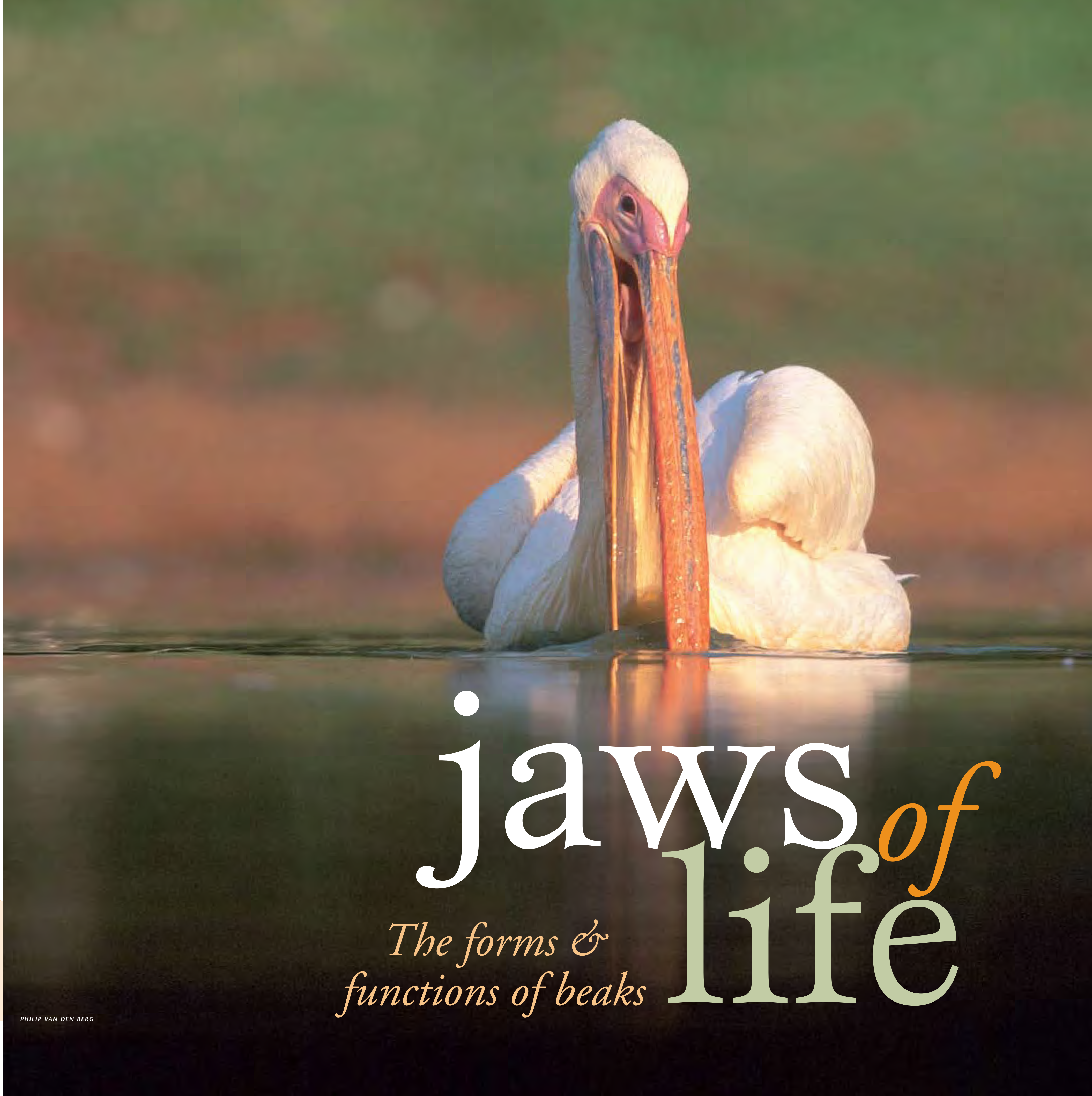
This adaptation was the feather. The feather as we know it today is an extremely intricate structure and it certainly did not miraculously appear in a finger-click of 'intelligent design'. Indeed, the function of the earliest feathers was not to facilitate flight but almost certainly to provide a degree of insulation to a group of dinosaurs that had developed partial warm-bloodedness (feathers would be a very 'bad plan' for a cold-blooded animal, retarding its ability to absorb heat from the sun).

From feathers to beaks

Whether they evolved for insulation or not, the proto-feathers set the stage for the theropod dinosaurs to conquer the air. It would have been a long process: the oldest theropod dinosaurs (the immediate ancestors of birds) evolved some 80 million years before the first birds, but some theropods survived as unfeathered dinosaurs contemporary with the first birds. Prior to becoming feathered, theropods almost certainly used their forelimbs (arms and hands) for handling, if not subduing their prey. However, as the feathering progressed, the forelimbs would have become less and less useful in this role, perhaps passing through a stage of functioning as giant flyswatters before eventually becoming redundant for catching or handling food.

So the role of the forelimb passed from one linked to prey handling to one entirely devoted to locomotion – flight. This is a classic example of an evolutionary compromise which, in order to persist, had to ensure that the benefits gained from the ability to fly exceeded the costs of sacrificing the forelimb to prey handling. Today, the benefits of flight are self-evident – birds are the most speciose terrestrial vertebrates. There are barely half as many species of mammals as birds, but of those, approximately a quarter belong to the one group of mammals that evolved powered flight, the bats. The key to success was mobility. This gave birds the wherewithal ▷

The beaks of pelicans, such as this GREAT WHITE PELICAN *Pelecanus onocrotalus* (right), have an adaptation shared with no other birds in the world – a modified lower mandible with a huge, distensible pouch. The pouch is so large that, in addition to the bird's catch (which may weigh more than a kilogram), it can hold almost 14 litres of water. Great White Pelicans typically fish in groups, beaks submerged in the water and with the pouches distended like a line of pink seine nets, herding shoals of fish.



jaws of life

The forms & functions of beaks

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The **SKIMMERS** (*Rhynchops* spp.), represented by one species in Africa, belong to the same family as gulls and terns. However, they have a spectacular beak adaptation that is used in a unique way. The lower mandible is 20–25 millimetres longer than the upper mandible, and it has grooves on its surface. Skimmers hunt in flight low over the water, with the lower mandible scything through it, striations parallel to the water surface to reduce drag. They search for fish by touch, and when the lower mandible touches prey, the neck snaps forwards and down, rapidly closing the mandibles and trapping the fish in the beak. To make the fish easier to hold, the upper mandible is slightly arched, like a nutcracker.

to escape the aftermath of the meteorite that turned out the lights for all other contemporary dinosaurs.

But taking to the air brought compromises with it beyond merely a change in use of the forearm. Birds can no more disobey the rules of aerodynamics than can an aeroplane. Aeroplanes have light and rigid bodies, and they have wings. Theropod dinosaurs had none of these, and avian evolution took time, involving processes such as fusion, reduction and pneumatisation (hollowing) of bones. These adaptations needed to take place over the whole body, including the head: theropods had heavy skulls and big, crocodile-like enamelled teeth. The first fully feathered birds hadn't quite got this completely right – the well-known *Archaeopteryx* still had enamelled teeth, and whether it was capable of powered flight is a moot point. Even 70 million years after *Archaeopteryx*, some birds still retained crocodile-like teeth.

That tooth-like structures in the beak can be beneficial to at least some birds is evident even today. Although no birds with enamelled teeth survive, the sawbill ducks, such as mergansers (*Mergus* spp.), have such structures to assist them in grasping their slippery fish prey. Rather than being enamelled, these are simple serrations along the margins of yet another body-lightening structure of modern birds: the beak.

Adapting the design

With the exception of rather few birds that catch their prey in their feet (raptors), stamp their prey to death with their feet (the Secretarybird) or use their feet to excavate buried prey (many gamebirds), birds rely on their beaks to catch and handle a wide diversity of food (although many use their feet to assist in the handling process).

Once the basic beak was in place, a whole new vista opened up for birds and their ability to fly allowed them to play with this opportunity across the planet. It permitted them to occupy food niches from the broad (generalists) to the narrow (specialists). Even small changes in beak structure allow bird species to exploit different food resources, some shared, some unique. This diversification, in conjunction with modification in wing structure (which influences where a bird can feed) explains why more bird species can co-occur than is the case for any other group of terrestrial vertebrates, including bats. The beak is evolutionary Plasticine of the most malleable kind.

This is illustrated best not so much by comparisons between species, which are often extreme, as by comparisons within species, which are more subtle. For most species, beak morphology determines what can be caught and what can be eaten. If two individuals eat different food, then the chances for competition between them (at least for food) are reduced. The most intense competition is likely to occur between individuals seeking exactly the same food, in other words, members of the same species. In the case of territorial species, the mated birds within a territory are likely to be the strongest competitors with each other for food, requiring that they defend a territory large enough to provide resources for both of them. The bigger the territory, however, the more energy must be expended in its defence.

In some cases, however, evolution has provided at least a partial solution to this conundrum. If males and females have differently shaped beaks and therefore eat different food, this may allow them to defend a smaller territory, leaving more energy available for other activities, such as breeding.

Some birds show differences in beak morphology between the sexes that have been linked to differences in diet – these include woodpeckers and oystercatchers. In the case of the latter, the males have relatively short, chisel-ended beaks, enabling them to remove limpets from rocks, while the females have longer, more pointed beaks, enabling them to extract worms from among mussels.

The bigger picture – interspecific variation

It is tempting to think of the relationship between birds and their food as a purely predatory one. This is true when birds are eating other animals, but does not necessarily apply to birds that are, for want of a better word, vegetarians. Many plants depend on birds for ▷

WOODPECKERS, especially the larger species such as Bennett's Woodpecker *Dendropicos bennettii*, are well known for their habit of hammering their beaks into tree trunks and branches in search of food, making a sound that sometimes can be heard more than a kilometre away. With the speed of the beak at impact being up to 0.7 metres per second, the question arises as to why woodpeckers neither damage themselves doing this nor end up needing headache pills. Several elements combine to prevent these problems. Firstly, impact forces are transmitted mostly below the brain case. Secondly, muscles attached to the base of the lower mandible are contracted before impact, and act as shock absorbers. Thirdly – a feature shared by birds in general – they have only small quantities of cerebrospinal fluid: if they did not, such fluid would risk sending dangerous shockwaves through the brain and down the spinal column.

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Female (left) *and male* (right) *African Black Oystercatchers have differently shaped beaks that allow them to exploit different food resources.*

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The **SOUTHERN DOUBLE-COLLARED SUNBIRD** *Cinnyris chalybeus* **(left, top)** and the **COMMON SCIMITARBILL** *Rhinopomastus cyanomelas* **(left, bottom)** both have thin, pointed, decurved beaks. But these serve very different functions. The sunbird's beak is adapted to fit into the flowers of nectar-providing plants, where they receive sugary food in exchange for pollination services. The scimitarbill's beak serves a different function altogether. Rather than acting as a pipette, it is a delicate pair of curved forceps used mostly to extract small invertebrates from under the bark of trees. Interestingly, the sunbird does eat some insects (especially when feeding chicks) and the scimitarbill occasionally feeds on nectar.

pollination, but they need to be selective about which birds visit them to transfer the pollen, because they need to maximise the probability that the pollen will be taken from the male plant to a female of the same species. There are many examples of 'co-evolution' between flower morphology and beak morphology, a good African example being the matching of the flower shape of *Erica* species with the beak shape of nectar-feeding sunbirds. Many species of *Erica* even have structures on the plants that make it easy for sunbirds to perch within reach of the flowers (because, unlike hummingbirds, sunbirds do not hover while they are feeding).

One step on in the plant life-cycle is the fruiting stage and, again, many fruiting plants depend on birds to disperse their seeds (the soft outer coating of the fruit being the reward that the bird receives for performing this service). Many frugivorous birds do not seem to be that fussy about which fruits they eat, with the result that frugivores show considerable variation in beak structure, from the short, strong beaks of barbets to the long, decurved beaks of hornbills. In these two instances, beak morphology might not have been as strongly driven by food as by breeding behaviour. A barbet that had a beak like a hornbill would struggle to excavate a nest, and a hornbill with a beak like a barbet would struggle to pass or receive food through its nest entrance.

Once birds eat other animals, however, the equation starts to take a different form. They become the hunter and their prey the hunted. Here we enter the realms of evolutionary arms races, with the prey trying to find means of avoiding capture or consumption and the predator trying to stay one step ahead. These, of course, are not conscious decisions, merely a consequence of selective removal of those that 'got it wrong' and/or advantages accruing to those that 'got it the most right'. Viewed from the point of view of the predator, there are various options to improve hunting success that may not involve the beak, such as where and how to search for food. But the beak can come into play well before prey are captured, as a searching tool. Many shorebird species, for example, probe for prey in the mud. Embedded near the tips of their beaks are sensitive receptors called Herbst Corpuscles. These are not touch detectors, but chemical scent detectors that allow the birds to determine whether prey are present in the immediate vicinity or whether they should give up the search and move elsewhere.

Beak morphology comes into play most conspicuously during prey capture, and subtle differences in the former can lead to large differences in the latter. Darters and cormorants, for example, are both moderately long-beaked underwater fish-hunters. However, the cormorant's beak is hook-tipped, whereas the darter's is pointed. Cormorants grab their prey between their mandibles, using the hook to prevent the prey slipping out of the beak, while darters spear their prey.

Beaks and migration

Many birds undertake seasonal migrations. In some cases, these journeys take them from one habitat to another and from one diet to another. In instances such as this, an evolutionary 'decision' needs to be taken as regards beak structure: should it be well adapted for a certain time of year or should it be a compromise that works adequately in all seasons, but perhaps not brilliantly in any one?

The Common Whimbrel *Numenius phaeopus* breeds on boreal moorland and tundra fringes, where it eats mostly the abundant terrestrial arthropods, the majority of which are caught at or very close to the soil surface. The elaborate curved beak seems of little obvious ▷

Cormorants **(opposite, top)** *and darters* **(opposite, bottom)** *are both underwater fish-hunters, but their beak designs differ – the cormorant's ends in a hook to prevent prey escaping, while the darter uses its straight bill to spear its victims.*

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The **GREATER FLAMINGO** *Phoenicopterus ruber* **(above, left)** and **LESSER FLAMINGO** *P. minor* **(above, right)** appear to have very similar beaks. Both are 'keeled' and contain lamellae for filtering food from the water (much in the manner of a baleen whale). The Greater Flamingo has a shallow-keeled beak, in which the two mandibles are of equal width, but even when the beak is closed, the two mandibles do not meet fully. In this species, the upper mandible is a shallow oval in cross-section. The Lesser Flamingo, by contrast, has a deep-keeled beak in which the upper mandible is triangular in cross-section and narrower than the lower mandible. When the beak is closed, the upper mandible slots neatly into the lower mandible.

The two species also have different lamellae. Those of the Greater Flamingo are designed solely for preventing prey escaping once in the mouth. Those of the Lesser Flamingo serve two purposes: some lamellae prevent food escaping, while others prevent food particles that are too large from entering the mouth. The Greater Flamingo can only control the size of food particles entering its mouth by altering the extent to which the beak is opened.

Not only do the beaks differ in their mechanical properties, but Greater Flamingos typically feed with their heads deeply submerged, while Lesser Flamingos strain food from close to the water surface. The result is completely different diets – Greater Flamingos eat mostly crustaceans, whereas Lessers are specialists on cyanobacteria (previously known as blue-green algae).

The beak of the **SHOEBILL** *Balaeniceps rex* **(above)** is a huge structure, resembling, as the bird's name suggests, a giant, closed clog. It can contain a massive volume of material, and is structurally reinforced. Its sheer eccentricity would lead one to suspect that this bird has an extremely specialised diet, but this is not the case: Shoebills eat fish, frogs, snakes and lizards, and occasionally the young of crocodiles and of other waterbirds. It seems as though the beak is primarily an adaptation to the thick, tangled aquatic vegetation in which the bird catches its prey. When hunting, the bird almost appears to collapse onto its beak when striking at prey, implying that the ultimate selective pressure behind the design is the simple need for brute force!

value in this situation – a much shorter beak would have been adequate. Yet if prey on the breeding grounds are easily caught, then the long beak may not be a significant handicap. During the non-breeding season, however, these birds move to coastal mud- and sand-flats where many of their prey, particularly prawns and worms, are quite deeply buried (and prawns live in curved burrows). Here, where there are many potential competitors for surface-dwelling or shallowly buried prey, the long, curved beak comes into its own. This suggests that, in the case of whimbrels, it is conditions on the non-breeding grounds that have provided the selective force favouring the long beak.

In New Zealand, another shorebird, the Wrybill *Anarhynchus frontalis*, has responded in the opposite way. This bird, the size of a small turnstone, is unique among the world's birds in that its beak bends approximately 20 degrees to the right. In the non-breeding season, it feeds alongside other shorebirds on coastal mudflats on North Island and it is hard to imagine how a fairly short, sideways-curving beak is any great advantage under these conditions. At the start of the breeding season, however, these birds move to nesting sites in large, stony river beds on South Island. Here the function of the bizarre beak becomes apparent. The birds feed extensively on fish eggs and caddis-fly larvae. These prey cling to the undersides of rocks, and the unique beak structure is perfect for their extraction.

Super-specialisation – is it a good plan?

Being super-specialised like the Wrybill does confer some advantages, not least potentially unique access to food resources. However, in evolutionary terms, it may also carry a high risk. Evolution, driven by natural selection, can only act on present-day conditions – it has no crystal ball with which to see into the future. Equally, there is a limit to the pace at which it can respond to changing conditions.

Among birds, almost all documented extinctions in the past 400 years can be attributed to human interference, such as persecution and habitat destruction. Nonetheless there are some birds, such as the Crab Plover *Dromas ardeola*, which, by virtue of their very specialised ecology (including a specialised diet), seem destined to be naturally rare. This condition has been termed the 'rarity trap', and it is one from which there is no obvious evolutionary escape should conditions change significantly.

Numerous eminent biologists have warned that the Earth is heading for the greatest mass species extinction of all time, an event precipitated by man-made changes to the planet. In terms of birds and their feeding apparatus, it can be predicted that the specialists, many of which are fairly recent products of evolution, will be the most vulnerable to a changing world. Whilst at first glance it might appear that there is no possible upside to this scenario, survival of generalists would leave some foundation on which evolution could act in the future, as has happened following previous mass extinctions. □

PETER RYAN

The **RED-NECKED PHALAROPE** *Phalaropus lobatus* obtains its food in a very unusual way. First it spins on its axis in the water, creating a vortex below its belly which drags tiny food items to the surface. Once the food is at the surface, the phalarope touches the tip of its very fine beak – with the mandibles slightly open – onto the water surface. A drop of water containing the prey is drawn into the beak by surface tension, requiring no sucking or tongue action on the part of the bird.

At the apex of the food and power chains are the big **EAGLES** which, like the hugely powerful Martial Eagle *Polemaetus bellicosus* **(right)**, are equipped with massive, hooked beaks. These, however, are not used in prey capture – they kill with their feet: the Martial Eagle can kill prey weighing up to eight kilograms. Obviously, prey of this size are far too large to swallow whole, and the primary function of the powerful beak is to tear the carcass into edible-sized chunks.

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