ALBERT FRONEMAN

thermal BUFFER

Forest birds reveal their physiological secrets

Avian biodiversity reaches its most spectacular levels in forested habitats at tropical latitudes. Often perceived as climatically benign and among the least challenging of habitats for birds to occupy (compared, for example, to deserts), life in tropical and subtropical forests can in fact be physiologically demanding. High air temperatures combined with oppressive humidity create stifling conditions, as anyone who has tramped through the forests of northern KwaZulu-Natal in 38-degree heat on a humid day can confirm. For birds living in open habitats along forest edges, these conditions are often combined with intense solar radiation while foraging.

The physiological challenges of very hot, humid weather arise from the fact that in these conditions birds effectively lose their primary defence against heat stress: evaporative cooling. Dissipating heat evaporatively through behaviours such as panting can take place only if the surrounding air is dry enough to absorb water vapour expelled by the bird. During periods of very high humidity, the gradient required for birds to offload heat is no longer there. Instead, heat produced by activity or gained from the environment is retained in the birds' tissues, causing body temperature to increase.

above *Forest birds like Red-capped Robin-chats have evolved wider thermal safety margins than species in other habitats.*

Remarkably little is known about body temperature regulation in hot conditions among birds inhabiting humid lowlands in the tropics and subtropics. The reason becomes evident when examining the history of avian thermal physiology, a field of scientific enquiry that largely emerged in the 1950s. When pioneering researchers like George Bartholomew and Bill Dawson sought environments in which to study the limits of birds' physiological capabilities, they naturally focused on deserts, inherently inhospitable environments posing severe physiological challenges to life. One notable exception, however, was Wesley Weathers, who studied the physiology of forest passerines in Panama in the 1970s and '80s.

Marc Freeman, a PhD student based at the University of Pretoria and co-funded by the FitzPatrick Institute, recently investigated the ways in which forest birds cope with heat. To do so, he compared the thermal physiology of birds from the coastal lowlands of northern KwaZulu-Natal to that of species from desert habitats in the Northern Cape and montane grasslands of the eastern Free State. The 20 lowland species included Red-capped Robin-chat, Olive Sunbird, Sombre Greenbul, Blue-cheeked Bee-eater and Yellow-rumped Tinkerbird, while Bokmakierie, Buff-streaked Chat, Pied Starling and South African Cliff Swallow were among the 19 grassland species.

Marc's data revealed several novel patterns. Resting body temperatures were slightly lower in forest species (averaging 39.8 degrees Celsius) compared to arid-zone species (40.6 degrees). At the upper end of the scale, however, lowland birds tolerated higher maximum body temperatures (45.6 degrees versus 44.7 degrees in desert species). The forest species thus have a greater scope, by approximately two degrees, for accommodating increases in body temperature above baseline levels. This can be thought of as a wider thermal safety margin, providing a more robust physiological buffer against the negative effects of severe, uncontrolled hyperthermia.

RICHARD DU TOIT (2)

above *Deserts are characterised by very dry air and the animals that inhabit them can rapidly dissipate heat by evaporation.*

above, left *High humidity in coastal lowlands impedes evaporative cooling.*

The finding that birds of coastal forests are more tolerant of hyperthermia than species inhabiting deserts came as a surprise. Most deserts are characterised by brutal summer heat and a scarcity of water and food, conditions widely thought to have driven the evolution of extreme physiological tolerances in the birds that do manage to eke out an existence. Moreover, the capacity to tolerate body temperatures far above resting levels also confers significant benefits in terms of reducing reliance on internal water reserves that would otherwise be needed for evaporative cooling. When Marc's study was published in the prestigious *Proceedings of the National Academy of Sciences*, we suggested this seemingly counter-intuitive finding might be related to the energy required by birds' tissues to produce molecules that protect cells from the biochemical effects of heat exposure. These molecules, called heat shock proteins, are thought to be expensive to produce, which might be problematic for birds occupying arid, resource-scarce environments but conceivably less so for forest birds.

But how exactly does the capacity to tolerate extremely high body temperatures benefit lowland birds under natural conditions? To answer this question, Marc designed an experiment in which he was able to control the humidity birds experienced during measurements of body temperature and related variables. He compared thermal physiology in dry air (approximating desert conditions) to patterns of body temperature regulation in moist air (simulating a very humid day in coastal forest).

The effect of humidity differed markedly among species from the various habitats. High humidity barely affected the performance of forest birds during very hot conditions, but severely compromised the ability of desert and grassland birds to cope with high air temperatures. The results also confirmed that tolerance of higher body temperature was indeed the major factor responsible for forest birds' greater capacity to cope with humidity. Humid conditions prevent evaporative heat loss and create a scenario where birds can sustain activities like foraging only if they can tolerate substantial increases in body temperature. Lowland birds' wider thermal safety margins, therefore, appear to have evolved to delay the onset of negative effects of hyperthermia and permit them to remain active for longer during hot, humid weather.

Marc's research has revealed that physiological adaptation in birds' body temperature has evolved in response to humidity, in addition to other environmental variables. Although we have barely scratched the surface of the thermal physiology of the birds inhabiting the world's most biodiverse regions, these insights from birds inhabiting the forests of South Africa's east coast are fundamentally changing our understanding of how body temperature differs among species and the consequences for birds' capacity to persist on a warming planet.

ANDREW McKECHNIE

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urban legends

Protecting penguins in a small coastal town

PETER RYAN (2)

With only 10 000 breeding pairs of African Penguins left in South Africa, Simon's Town is more than ever the place to be, whether you are an African Penguin and looking for a place to breed or you want to see this beautiful species in the wild. The Simon's Town penguin colony now holds about 10 per cent of the South African breeding population of this Endangered species, the only penguin that can be seen in the wild in Africa.

Simon's Town is a special place for African Penguins. Since they began to breed there in the 1980s, they have done well compared to many of the other colonies, which have seen dramatic declines in recent years. They seem to find enough food in False Bay to breed and to raise their chicks and, in general, their close proximity to hundreds of tourists each day doesn't appear to disturb them.

above *A familiar sight in Simon's Town, African Penguins seem oblivious to the dangers posed by street life.*

The penguins are watched not only by the tourists who visit the colony and by television viewers around the world who follow the popular series about the birds, but also by a dedicated group who keep an attentive eye on these birds: the Penguin Rangers.

Simon's Town's Penguin Rangers form part of a collaboration between the City of Cape Town and SANCCOB that is supported by NatureConnect and works closely with SANParks. The rangers check the nests regularly and conduct breeding and moult counts to monitor the local penguin population and assist with several research initiatives.

The penguins are being microchipped as part of a nationwide project and two ground readers monitor the birds as they enter and leave the colony, providing crucial information about breeding patterns and the duration of foraging trips and, ultimately, their long-term survival. The data help researchers to identify important foraging areas and monitor breeding success in different types of nest and habitat as part of a climate change study. Since similar studies are carried out in other colonies, mainly on islands, across the African Penguin's breeding range, the information from Simon's Town is an important piece in the puzzle of understanding current threats to the species and trying to prevent its extinction.

However, some threats are very particular to breeding on the mainland – and to Simon's Town. Every day, the Penguin Rangers have to deal with tourists trying to get the perfect photograph, which often involves them overstepping boundaries and not respecting fences or keeping a safe distance from penguins on beaches. Dog owners who don't think their hound could do any harm to penguins should be aware that the rangers regularly find penguins that have been attacked by dogs, often with fatal consequences.

The behaviour that has transformed the birds into Netflix celebrities also poses a major threat to them. African Penguins love to walk the streets of Simon's Town, but unfortunately they are not very street-wise. Significant numbers are killed every year in the town, either when crossing roads – especially in the early morning and late afternoon when they commute between the sea and their nest sites – or when they hide or rest under parked cars. The roadkill victims are usually healthy adults that form the backbone of the breeding colony and would produce the next generation. The Penguin Rangers constantly try to dissuade the penguins from moving into residential areas by relocating them back to safe breeding sites along the coast. The City of Cape Town is improving fencing along the coastline to limit the high mortality of the penguins and has erected signboards alerting tourists to check for birds resting under their cars before they drive away.

JEAN DU PLESSIS

above *Simon's Town's penguin guardians. (Front, left to right) Arne Purves and Mashudu Mashau (City of Cape Town: Coastal Management); Shanice Mabuza (student ranger). (Rear, left to right) Penguin Rangers Kashiefa Amos, Vardaman Hahndiek and Mikaela Slier.*

above, left *The penguins have become used to the attention of sometimes over-eager tourists.*

Although the Penguin Rangers have their hands full trying to protect the penguins from caracals, dogs, cars and sometimes ignorant tourists, the location of the Simon's Town penguin colony is also an advantage, both for the species and for conservation in general.

From tracking studies, we have learnt that African Penguins breeding in Simon's Town stay within False Bay when feeding and provisioning their chicks. The characteristics of the bay and the lack of industrial fishing pressure seem to make this area ideal for foraging penguins. They also have a variety of nesting habitats to choose from, from the sunny beachfront to shady forest areas, and in general they breed relatively successfully in Simon's Town. In the event that heat or storms threaten eggs or chicks, the Penguin Rangers are there to come to the rescue and take them to SANCCOB, where they are cared for before being released back into the wild.

Being such a tourist attraction can sometimes be a problem for African Penguins, especially in summer when they undergo their annual moult and are more sensitive to disturbance. However, the fact that thousands of tourists come to Simon's Town to see the penguins is also a great opportunity to educate people about the importance of penguins, a healthy ecosystem and how their own behaviour can make a positive difference.

In addition, the colony has huge added value for Cape Town's economy. Not only do restaurants and souvenir shops in Simon's Town benefit from people coming to watch the penguins, but South Africa's tourism industry relies heavily on these birds. People travel to South Africa to see the penguins and the Simon's Town birds are a major attraction on the Cape Peninsula. The findings of a report commissioned by the City of Cape Town in 2018 revealed that visitor numbers increased threefold, from 310 000 in 2006 to 930 000 in 2017. As a tourism destination, the colony supports 180 permanent jobs, but its impact on livelihoods is far more extensive: 885 Cape Town jobs are associated with it in some way.

So why not consider a visit to a small coastal town where you can see a threatened species without too much hassle and at the same time support the local economy. But please just remember to look under your car before driving off!

KATTA LUDYNIA
SANCCOB

SANCCOB relies on donor funding to maintain the Penguin Rangers in Simon's Town and other penguin colonies. If you would like to support their work, please consider donating to SANCCOB. *sanccob.co.za*

PETER RYAN

mating moves

Meek male albatrosses don't get it

Albatrosses are renowned for their long-term monogamy. They are often portrayed as 'mating for life', although this typically means for the life of their partner, not having a single true love. When an albatross loses its mate, it almost always tries to breed again with a new partner. However, divorces do occur. They are fairly frequent in the smaller *Thalassarche* mollymawks and even occur occasionally in the *Diomedea* great albatrosses. Two recent papers investigate the causes and consequences of divorce among the well-studied Wandering Albatross population on Possession Island in the Crozet Archipelago, south-east of Africa.

In the first paper, Sun et al. (2022, *Ecological Monographs*, doi: 10.1002/ecm.1522) show how over the past 60 years, divorce has been more common among female than male Wandering Albatrosses. This is a consequence of the greater mortality of female Wandering Albatrosses on long-lines. Females usually forage farther north than males and thus overlap more often with long-liners, resulting in greater bycatch mortality. This leads to males being widowed more often than females and thus results in an excess of males in the population. The larger number of males provides females with more mating options, potentially giving them the opportunity to take advantage of this imbalance through strategic divorces.

above *A recent study suggests that old male Wandering Albatrosses are prone to being displaced from their long-term pair bonds by younger, more aggressive males.*

However, there is little evidence of female choice in the process. If divorce is adaptive, we would expect females experiencing low breeding success with their current partner to stray. Yet the opposite was found – females that divorced tended to have higher than average breeding success prior to the divorce. Also, there is no change in breeding success after divorce and female survival tends to decrease following a partner swap, so females do not benefit from a change of mate. As expected, divorce is more likely among newly established pairs; once a pair gets into a groove, they are less likely to switch partners. However, there is a tendency for older males to be more likely to divorce.

The study concluded that most divorces are non-adaptive and result from a new male displacing the existing partner. This is consistent with the seeming lack of benefit to females arising from extra-pair paternity. Some 10 to 20 per cent of Wandering Albatross chicks are fathered by a male other than the social father, but studies to date have not revealed any significant advantage to females in terms of improved breeding success or greater genetic diversity in their chicks. A previous study at Possession Island concluded that most, if not all, extra-pair copulations were forced, again resulting from the large numbers of unmated males in the population (Jouventin et al. 2007, *Ibis* 149: 67–78).

Competition among males for access to females explains why older, less vigorous males might be more easily displaced and thus suffer a higher divorce rate. But other factors might also play a role. Field biologists have long known that albatrosses vary in temperament; some parents are unperturbed when you check their egg or small chick, whereas others are nervous or aggressive. The second study (Sun et al. 2022, *Biology Letters*, doi: 10.1098/rsbl.2022.0301) explores the impact of bird personality on the likelihood of divorce.

Since 2008, researchers have used the responses of Wandering Albatrosses breeding at Possession Island to score the birds' 'personality'. Using these data, they show that timid males are much more likely to divorce than bold males. They conclude that aggressive males are able to displace more timid males and thus monopolise mating opportunities.

However, what is perhaps most interesting is how divorce appears to be more common among Wandering Albatrosses at Possession Island than at other long-term study sites of the species. A few years ago I searched the breeding histories of Wandering Albatrosses at Marion Island and struggled to find a single case of divorce, even though there is a similar excess of males and occasional forced extra-pair copulations have been observed. It is not clear why there might be this difference.

PETER RYAN

RICHARD DU TOIT

owl origins

Into the black (and back)

A 55-million-year-old fossil owl indicates that the first owls hunted by day and only subsequently became nocturnal.

Owls are one of the most distinctive groups of birds. Their toes and claws are adapted for killing and their largely nocturnal hunting habits have resulted in major modifications to their visual and auditory systems. To maximise their vision in low light levels, owls have evolved massive, forward-facing eyes that are fixed in their sockets. Owls' ears also are larger than those of other birds and in some species are asymmetrical to allow them to hunt in complete darkness. Linked to these adaptations, modifications to the neck vertebrae allow the head to rotate up to 270 degrees, which compensates for their fixed eyes and assists with locating the source of sounds.

Both these sets of adaptations result in distinctive skeletal features that make it fairly easy to identify owls from fossil remains. As a result, we know that owls were among the first carnivorous birds to evolve in the radiation of modern birds that followed the demise of the non-avian dinosaurs, with the earliest owl fossils dating back more than 60 million years. However, very few of these early fossils preserved any head bones. Now a fossil owl discovered in the UK's London Clay Formation from 55 million years ago provides new insights into the early evolution of owls (Mayr and Kitchener 2022, *Ibis* doi: 10.1111/ibi.13125).

The most interesting finding is that the bird, named *Ypresiglaux michaeldonaldsi*, shows the raptorial leg and foot structure of an owl, but lacks several of the characteristics typical of a nocturnal lifestyle. Its skull has a large supraorbital spur on the lachrymal bone, which protects the eyes of falcons and hawks that kill prey with their beaks. However, this feature has been greatly reduced or lost by modern owls because it is incompatible with their very large, forward-facing eyes. Similarly, the skull shows no sign of an enlarged auditory apparatus and the vertebrae are not modified to allow extra head rotation. In short, it appears as though the first owls were diurnal raptors.

Two hypotheses might explain their switch to a predominantly nocturnal hunting mode: to benefit from novel foraging opportunities or to avoid competition with other predators. The former supposes that owls started hunting at night to take advantage of the diversification of moths (nocturnal butterflies) some 40 million years ago, and/or murid rodents some 20 million years ago. But would a marked increase in nocturnal prey drive all owls to become nocturnal? To me, a more plausible explanation is that they were pushed to forage at night by the evolution of other diurnal raptors. We know that hawks and falcons evolved after owls and their appearance might be responsible for the owls' switch to hunting at night.

Of course, not all modern owls are exclusively nocturnal. A few species are active during the day, such as the Northern Hawk-Owl and Short-eared Owl, as are several *Athene* and *Glaucidium* owls. Because these species share the structural adaptations for nocturnality with other owls, they are assumed to be secondarily diurnal. Another fossil discovery sheds some light on this evolutionary reversal.

Li et al. (2022, *PNAS*, doi: 10.1073/pnas.2119217119) describe an exquisitely preserved, fairly small (30-centimetre) fossil owl *Miosurnia diurna* from the Liushu Formation in Gansu Province, China, that lived between six and nine million years ago. The owl's eye structure is typical of a diurnal bird, suggesting it hunted by day. The fossil even contains evidence of its last meal – a small vertebrate – and the authors surmise that the owl fed on rodents in the arid steppe habitat that characterised the area at this time. It shared this niche with a large kestrel, *Falco hezhengensis*, a fossil of which has been found to contain the jaw of a jerboa (see Li et al. 2014, *Auk*, doi: 10.1642/AUK-13-245.1). They conclude that diurnal activity in owls may have evolved when the climate became cooler and dryer, creating open grasslands with large numbers of diurnal rodents.

PETER RYAN

new endemic

Red-winged Francolin

MAANS BOOYSEN (2)

above *Red-winged Francolin in the Rietvlei Nature Reserve, Gauteng, South Africa.*

above, left *Crawshay's Francolin on the plateau in the Nyika National Park, northern Malawi.*

It is always exciting to know which birds are endemic to an area. Endemism is where a species' range is localised to a defined geographic location, such as an island, country or other specific zone, and the species is found nowhere else on earth. The status of being endemic carries various connotations, from being the only place where one can see that species in the wild to carrying special responsibility for the conservation of sustainable populations of that species. Fundamental to the conservation of biodiversity is to understand the currency of conservation (which in essence are the species) and to recognise which species can act as flagships for their preferred habitats and thus play a role as umbrella species to help secure the viability of other species against human-induced threats in the landscape.

Recent research into the classification of spurfowls and francolins based on morpho-behavioural and genetic evidence has suggested a variety of changes to their taxonomy that are important for their conservation. One of these taxonomic changes is the elevation of the subspecies of the Red-winged Francolin *Scleroptila levaillantii crawshayi* to full species, Crawshay's Francolin *S. crawshayi*. Crawshay's Francolins are found north of the Zambezi River, occurring in Angola, Zambia, the Democratic Republic of the Congo, Malawi, Tanzania, Kenya, Rwanda, Burundi and Uganda.

Comparing the appearance of the two species in the accompanying photographs you can see that the Red-winged Francolin lacks Crawshay's Francolin's prominent white collar that extends from the base of the bill down the sides of the neck and meets below the white and orange throat patch. The black-and-white collar of the Red-winged Francolin is also more extensive on the lower neck and upper breast than that in Crawshay's Francolin.

The good news emanating from that research is that the Red-winged Francolin now enjoys the status of being endemic to South Africa and Eswatini. It is found in the eastern parts of South Africa and western Eswatini, where it thrives in rank, vigorous highveld grasslands, usually over deep soils. It is more sensitive to the burning or grazing of grasslands than other members of the red-winged group of francolins. In heavily grazed and frequently burnt grasslands, it can be restricted to wetland fringes and rocky outcrops.

There are numerous examples of local declines in its numbers and confirmed absence in areas of apparently suitable habitat where annual burning and overgrazing occur, as well as in unburnt moribund grasslands. However, grassland management that includes biennial burning and light grazing, particularly by wild herbivores, provides sanctuaries for this species. Other major threats are expanding commercial forestry and the damming or draining of wetlands.

Fortunately, there are secure habitats in various formally protected areas, including the Maloti Drakensberg Transfrontier Park, a World Heritage Site in KwaZulu-Natal; the Mkambati Nature Reserve, which is almost at sea level on the Pondoland coast in the north-eastern Eastern Cape; the Verloren Vallei Nature Reserve near Dullstroom in Mpumalanga; and other reserves across to the Rietvlei Nature Reserve in Gauteng. This protection bodes well for maintaining viable populations of Red-winged Francolins and is important because the francolins act as a flagship species for these sensitive grasslands and play a role as an umbrella species for other grassland birds in these areas.

ROB LITTLE

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