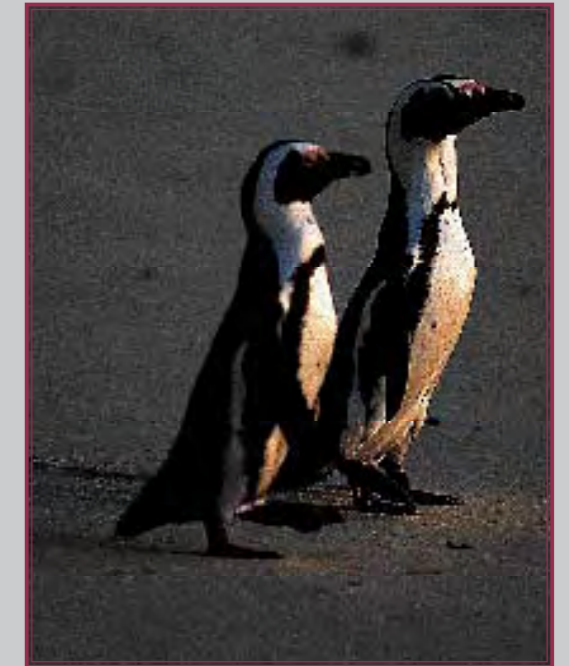


Dinner jacket strategies

Why Jackass Penguins wear striped tuxedos!



One of the main reasons for the enormous popular appeal of penguins is the way in which their coloration gives them a comical similarity to pompous old men, waddling about resplendent in formal suits.

But Africa's endemic Jackass Penguin – and other species in the genus *Spheniscus* – have changed the dress code. They differ from all other penguins in having bold black and white stripes on the head and breast.

Peter Ryan explains why the birds have this conspicuous pattern, and how they make the difficult transition from juvenile to adult plumage.

A group of adult Jackass Penguins emerge from the sea after a successful day's foraging. Their boldly striped plumage plays an important role in catching their fish prey.

PHOTOGRAPHS: PETER PICKFORD/FOCAL POINT

What determines the colour of a bird's plumage? Typically, coloration is a compromise between a number of selection pressures. For example, the need for sexual or social signalling often conflicts with the requirement for camouflage to avoid detection by both predators and prey. This accounts for many birds having concealed signals, such as white outer tail feathers, which are visible only when the tail is fanned. Attempting to disentangle the many factors that combine to determine a bird's coloration can be a fascinating challenge. The problem is complicated still further because in many instances the evolutionary forces that have shaped a bird's coloration occurred in the past and thus are not apparent when considering only the present situation.

Seabirds are one group where the evolution of colour appears to be fairly clear-cut. They are rather uniform in terms of colour, with virtually all species having plumage which is a combination of white, black, grey or brown. Most are darker above than below, which offsets brighter illumination from above. This colour pattern, which is widespread among animals, is termed countershading. Perhaps more importantly, when sitting on the sea, birds are least visible to potential predators if they are dark above and white below. This is especially important for penguins as they have to avoid predators such as seals and sharks without the option of flying away. It is assumed to be the reason why all penguins have black backs and white breasts.

PETER STEYN



The Jackass Penguin *Spheniscus demersus* (and others in the genus in South America) differs from other penguins in having bold, alternating black and white stripes along the side of the head and breast. This pattern makes the Jackass Penguin conspicuous when swimming. Why has it evolved this pattern? It is not as though it lacks predators – we know that both fur-seals *Arctocephalus pusillus* and sharks prey on the Jackass Penguin. Both sexes have the same plumage, so the bold pattern is unlikely to be the result of sexual selection. What other reason could there be?

Spheniscus penguins have another common characteristic – they all feed on pelagic schooling fish such as anchovies *Engraulis japonicus* and pilchards *Sardinops ocellata*, whereas other penguins feed primarily on crustaceans, squid or non-schooling fish. And herein lies the reason for the conspicuous coloration of the Jackass Penguin.

Its fish prey occur in loose groups, but react to predators by forming dense, highly polarized schools which make it hard for predators to single out targets. The Jackass and other *Spheniscus* penguins use their conspicuous coloration to manipulate fish behaviour and thus make them easier to catch.

Trials with captive fish have shown that fish schools break up more frequently and for longer when exposed to models with the boldly striped pattern of the Jackass Penguin than they do when tested with neutral or 'standard' penguin models. It is during this crucial, depolarized

state that fish are vulnerable to predators. The Jackass Penguin typically feeds in small flocks which co-operate to disrupt fish schools. Groups of penguins circle prey fish, with birds ready to peel off from the circling group and grab individual fish which pass up through the disorganized school. This behaviour has been observed in the field and is supported by the fact that fish taken by penguins have bite marks just behind the head, inflicted by a bird approaching from below the fish.

This explains the coloration of the adult bird. But the Jackass Penguin doesn't start out boldly patterned. Fledglings leave the nest and go to sea in a plumage which is the epitome of camouflaged countershading.

Left The Adelle Penguin is the archetype of a cartoon penguin in its tuxedo. All penguins are black above and white below, but adult *Spheniscus* penguins, such as the Jackass, are unique in having conspicuous lateral stripes.

Right A juvenile Jackass Penguin that has partially moulted its head to acquire the characteristic adult plumage pattern. Only a minority of juveniles undertake this moult, and most that do only attain the conspicuous white 'C' on the ear coverts. The Jackass presents the only known instance of a penguin species not moulting all its feathers at once.

Below The adult Jackass Penguins are characterized by both sexes having bold black and white stripes on the head and breast, whereas the juvenile (left) is a classic example of countershading for camouflage.

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Magellanic Penguins (above) have double breast bands, making them even more conspicuous at sea. A few Jackass Penguins (such as the bird below, centre back), also have double breast bands; it is not known whether this unusual trait is inherited, but the proportion of birds with double breast bands varies between breeding colonies.



With a maximum swimming speed of five kilometres an hour, they are much slower than are adult birds (see box, page 50), and are incapable of catching schooling fish which swim at 8–10 kilometres an hour. As a result, young penguins feed on slow-moving, solitary prey such as larval fish and pipefish. For fledglings, camouflage is essential both to minimize the risk of predation and to allow them to sneak up on their prey.

The challenge for the young penguins is to make the transition from slow-swimming, solitary-feeders to fast, efficient group-feeders taking high-quality prey species. During their first year at sea, young penguins gradually learn to swim faster and attain greater manoeuvrability. Any gradual plumage transition is ruled out, however, because penguins moult all their feathers at once.

The problem is made more acute by the fact that adults discriminate against birds in juvenile plumage. Watch a beach party of penguins for a few minutes and you realize that juveniles are second-class citizens. Adults pick on them much more than they do on other adults, and juveniles seldom initiate aggressive interactions and almost invariably back down when challenged by an adult. In order to test whether head pattern is the main factor mediating this aggression, researchers painted one side of the heads of adult birds into the uniform grey juvenile plumage, and left the other side bold black and white. As expected, aggression was directed more often to the juvenile-painted side of the head than to the adult side.

Increased aggression against birds in juvenile plumage is rather unusual. Most birds have a discrete juvenile plumage or, in dimorphic species, have young birds that resemble females, specifically to reduce aggression from adults. In the case of the Jackass Penguin, however, it makes sense for

adults to be overtly aggressive towards young birds because it pays them to exclude young birds from their feeding groups. Having naïve, drab birds in adult feeding groups would dilute the disruptive effect of conspicuous adult plumage. Sure enough, the proportion of juveniles in adult flocks at sea is much lower than expected, given the proportion of juveniles in the population.

One-year-old penguins find themselves in a Catch-22 situation: they need to switch to a high-quality diet to accumulate enough reserves to survive the enforced fast associated with a complete moult, but they cannot join adult feeding groups because of the stigma of their youthful coloration.

What can the juveniles do? Jackass Penguins do something that no other penguins are known to do: they undertake a partial moult into adult plumage. Conventional wisdom has it that penguins are constrained to replace all their feathers at once. This is because they cannot afford to have gaps in their plumage which dis-



GENTOO PENGUIN PETER STEYN

against cold water and because moulting severely increases drag, reducing swimming speeds (see box). Juvenile Jackass Penguins apparently haven't heard this, and they undergo a partial head moult while at sea. They apparently can get away with this indiscretion because the head is not in constant contact with the cold, energy-sapping water. Also, they apparently replace only a few feathers at a time and thus minimize the increase in drag.

Why should young birds go to all this effort? We know from watching interactions among penguins in beach parties that juveniles with moulted heads are subject to less harassment from adults than are those that haven't moulted. It seems likely that this translates directly into access to

Each penguin species has a unique head pattern. These almost certainly play an important role in species' recognition during mate selection, but it is not a coincidence that these unique patterns are located on the head. The head is the most visible part of swimming birds, and these patterns are thought to allow birds to identify those of the same species at sea. Alcids, the northern hemisphere ecological equivalent of penguins, also tend to have species-specific head and bill markings.



ROCKHOPPER PENGUIN PETER RYAN

adult feeding groups. The extent of head moult is not uniform – some juveniles moult almost the entire head, acquiring a full adult head pattern, whereas others only moult a white head stripe. The degree to which adults accept juveniles is directly related to the extent of the head moult.

Are adults being deceived into letting these juveniles into their feeding groups? Or are juveniles demonstrating that they have qualified to join adult groups, and that by moulting their heads they are displaying a 'badge of fitness'? The real situation probably lies between these two extremes. Only about a quarter of juveniles undertake a head moult at sea – presumably that resulting from the energetic cost of reduced insulation and increased drag. In this sense the ability to moult some or all of the head feathers is an honest reflection of fitness. If you like, only the strongest, fastest juveniles can afford to undertake a head moult, and thus are likely to be less of a liability in group-feeding situations. At the same time, however, adults rely on the bold, striped pattern of group members to manipulate fish schooling behaviour, and thus the juveniles that gain admission to adult feeding groups gain something of a free ride, because they typically lack the bold flank and breast stripes.

Whatever the balance of honesty and deception, the



EMPEROR PENGUIN PETE OXFORD



JACKASS PENGUINS

GERALD CUBITT

When it comes to swimming prowess, penguins are the bird world's gold medallists. The largest living penguin species, the Emperor Penguin *Aptenodytes forsteri*, holds the records for both the longest and deepest dives. Individuals have been observed to remain under water for up to 18 minutes, reaching depths of more than 260 metres. Less is known about maximum swimming speeds, but these are thought to exceed 25 kilometres an hour in short bursts.

Although not quite attaining these high standards, the Jackass

Penguin is no slouch in the swimming stakes. It is known to dive for at least four minutes and down to depths of 130 metres, although most foraging occurs in water less than 30 metres deep. Maximum swimming speeds vary with age and bird condition. Fledglings barely manage five kilometres an hour, juveniles get up to 10–12 km/h, whereas adults with fresh plumage can achieve 19 km/h. Adult swimming speeds decrease after moulting because older feathers create more drag, and breeding birds average 12–15 km/h.

Actively moulting birds are severely handicapped by their loose, old feathers and only swim at four kilometres an hour from the start of the moult until more than 70 per cent of the plumage has been replaced. Thereafter their maximum speed increases to about 10 km/h. Birds have to go back to sea and rebuild muscles depleted by the rigours of enforced fasting during moult before they can start setting speed records again.

These swimming speeds are not maintained over long distances. Breeding birds average five kilometres an hour while

commuting to and from feeding areas. Because breeding birds return to feed their chicks every day, this travelling speed restricts them to within a 25-kilometre radius of the colony. Compared to seabirds that can fly, penguins are severely constrained in terms of their foraging range and thus bank on food resources being reliably available in the vicinity of breeding islands. Despite this apparent limitation, penguins are extremely successful, accounting for up to 80 per cent of bird biomass at many breeding islands in the Southern Ocean. □