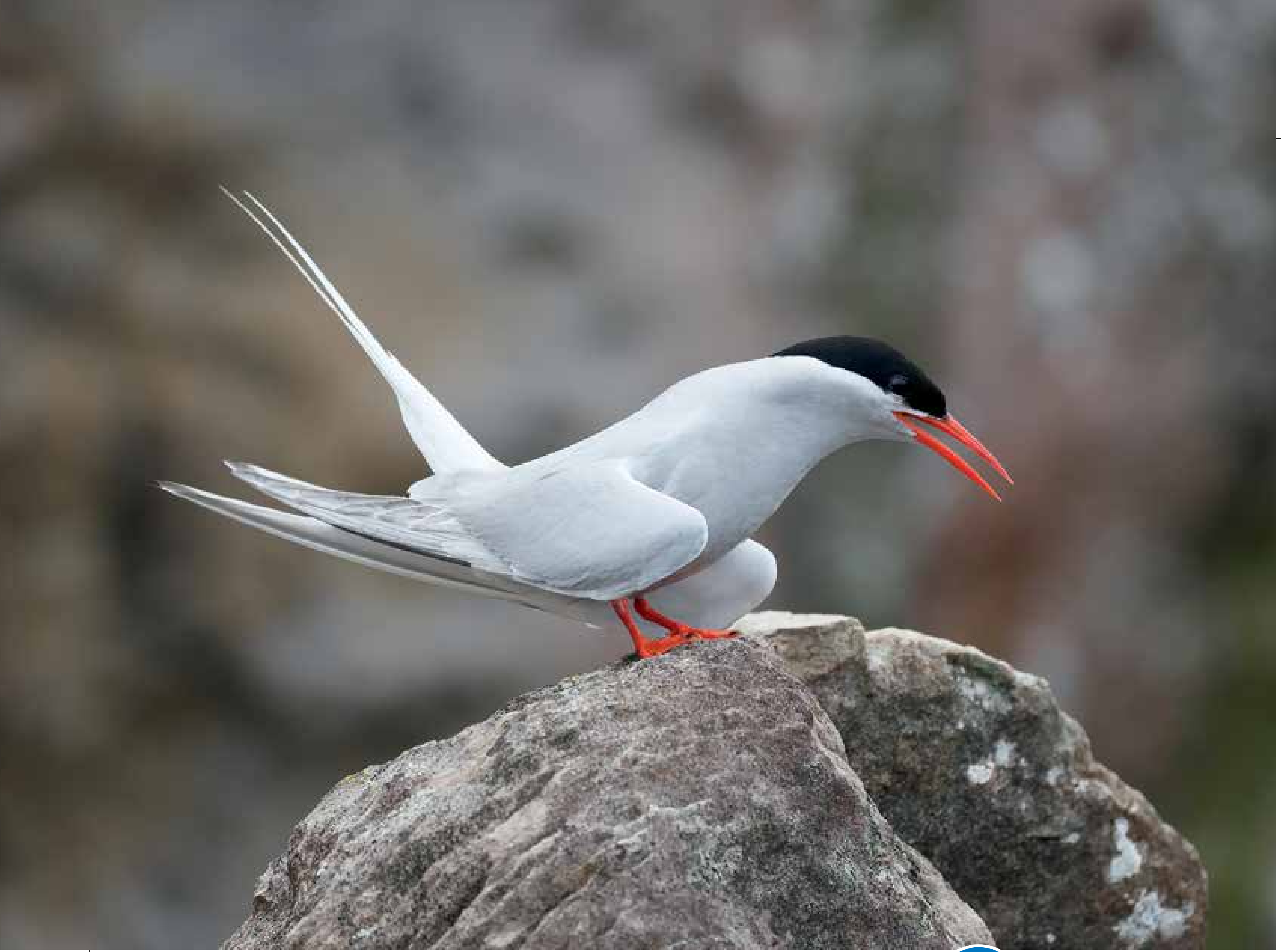
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stay OR go?

Migration as an evolutionary driver

TEXT **PETER RYAN & MICHELLE VRETTOS**

Birds are the most mobile organisms on the planet. Their ability to fly vast distances enables them to exploit predictable, short-term peaks in food availability. Almost one fifth of all birds undertake regular movements, usually tied to seasonal cycles. However, such large-scale movements also incur risks from commuting across the landscape. The balance between these costs and benefits determines who stays and who migrates. Recent studies suggest that migration promotes speciation, principally through the formation of sedentary daughter species. Here we highlight some examples and speculate how rapid global change might affect this process.

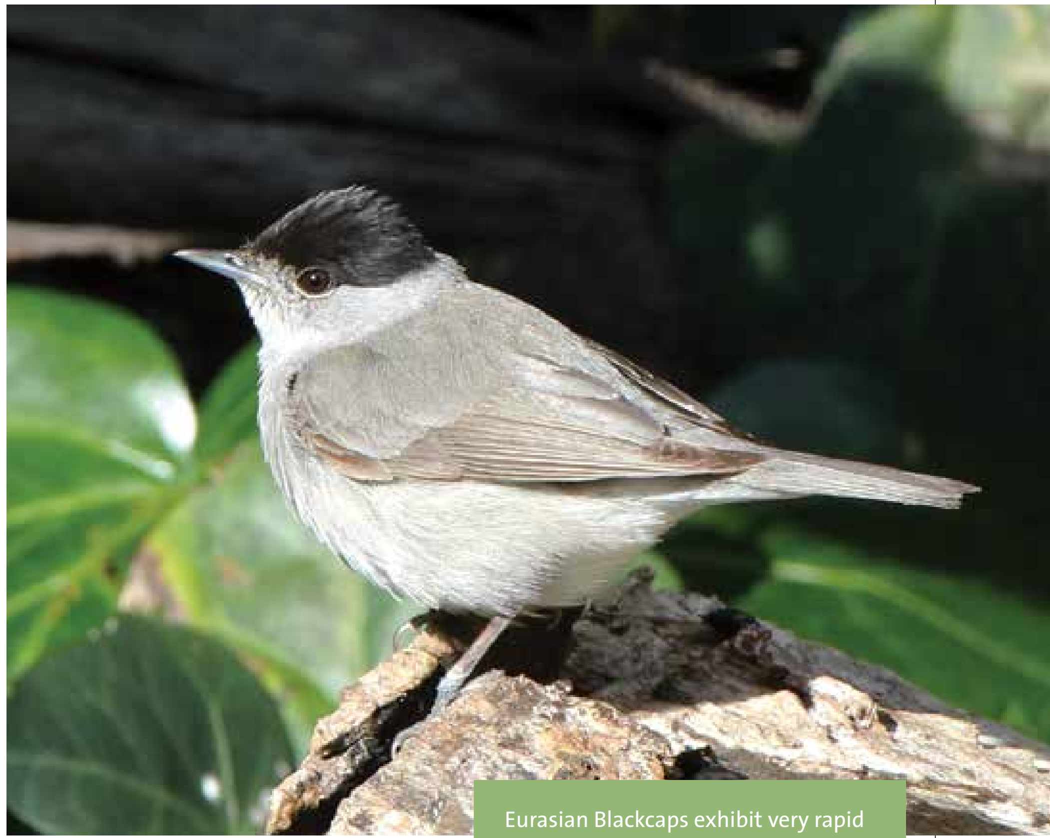
Migration has long fascinated people and considerable effort has been devoted to learning how birds migrate. We marvel at the physiological adaptations that enable Bar-tailed Godwits to fly nonstop for eight days from Alaska to New Zealand without eating or drinking. We have determined the range of cues that birds use to navigate to return to the same breeding and wintering sites year after year. We have demonstrated that the migratory urge is inherited, with genes coding for the direction and duration of migration. However, we know that the risk of being blown off course during a young bird's initial migration can be greatly reduced by travelling with more experienced individuals and we have even used small planes to establish new migration routes for threatened species. But why do birds migrate in the first place?

Why migrate?

The proportion of migratory species varies predictably with latitude, ranging from more than 70 per cent of species in polar regions to barely 10 per cent in the tropics. Migration is particularly important at high latitudes because of the marked difference in day length between summer and winter. Primary production is driven by photosynthesis, which requires sunlight, and longer days increase temperatures, which promote faster growth rates of plants and invertebrates on which birds depend. Thus high latitudes typically experience a large peak in food availability in summer, followed by a dearth of food in winter, when low temperatures also greatly increase the cost of thermoregulation. Birds are well suited to exploit such seasonal peaks in food availability because they can migrate to more benign areas in winter.

The seasonal signal is more extreme in the northern hemisphere due to the greater amount of land in the north. This results in more continental climates than in the southern hemisphere, where the extensive oceans buffer seasonality. As a result, at least at lower latitudes, the proportion of migrants tends to be less in the south than in the north. Also, in the south, rainfall is often more important than temperature in driving migration, although the underlying cause is the same; rainfall triggers a flush of food, which migratory birds exploit. However, rainfall is more erratic than seasonal changes in temperature and so migration among many southern hemisphere species is less predictable than among their northern counterparts.

Another consequence of the much greater amount of land in the northern hemisphere is that most migrant birds breed in the north and migrate south in winter. There are plenty of short-distance migrants within the southern hemisphere, but only a few landbirds move beyond the tropics. Even among seabirds, which are more diverse in the south, more trans-equatorial migrants breed in the northern hemisphere. It is only among *Pterodroma* petrels that >


TREVOR HARDAKER

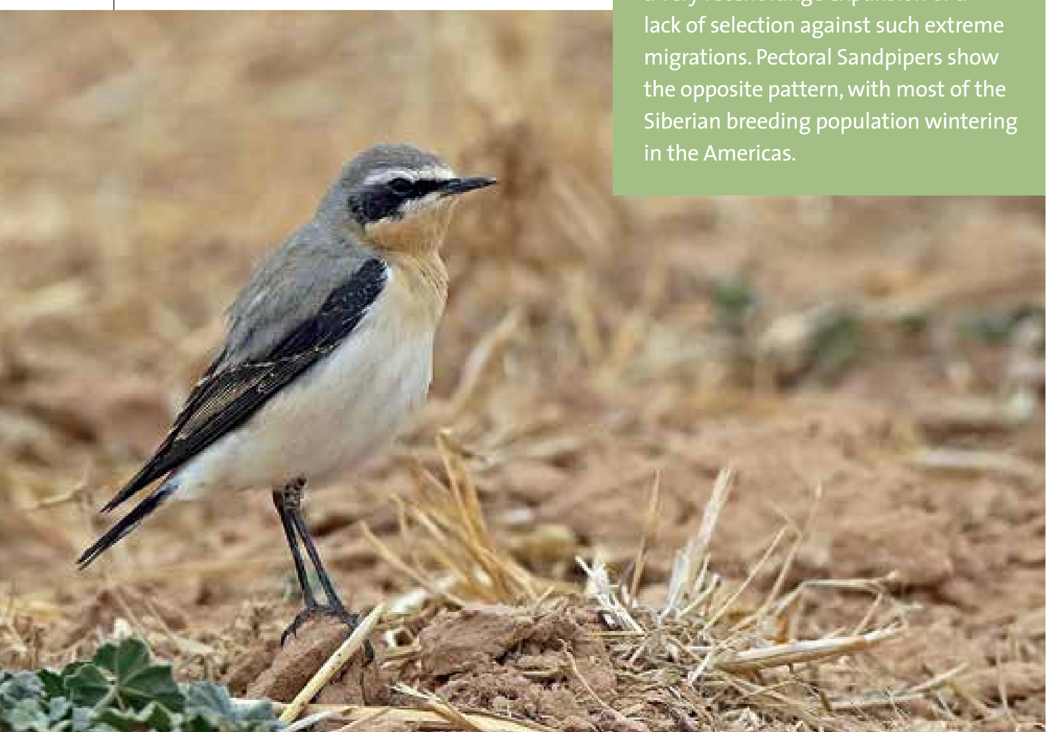
Eurasian Blackcaps exhibit very rapid shifts in migration behaviour. Over the past few decades, the arrival dates of migrants on their breeding grounds have advanced by several weeks and departure dates have been delayed in many populations, linked to ongoing climate change. Birds breeding in central Europe traditionally wintered in Africa or southern Europe, but increasing numbers now move to the UK in winter, where they are supported in part by bird feeders. Interestingly, when they return to their breeding grounds, they almost always breed with a partner from the same wintering area, resulting in the potential for further differences between the two populations to accumulate. At the same time, the migratory urge of blackcaps in southern Germany has almost halved over the past few decades and experiments with captive birds suggest that residency might soon evolve in this entirely migratory population if there is ongoing selection for shorter migration distances.

there is a strong southern hemisphere bias, with nine species breeding in the south and wintering in the north, compared to only two that breed in the north and winter in the south.

Ecologists and physiologists have argued whether migration results more from the seasonal variation in food availability or the greater costs of thermoregulation in winter. The proportion of migrant species is closely tied to mean winter temperatures in both hemispheres and both factors probably play a role, but food appears to be more important. Aerial insectivores, such as swallows, swifts and nightjars, are particularly prone to migrate, as are cuckoos that rely on caterpillars, because their food is highly seasonal. By comparison, woodpeckers are able to persist year round even in high-latitude forests because their insect prey is protected under bark. Woodpeckers also benefit thermally from roosting in cavities. Phil Hockey's excellent paper on the patterns and correlates of bird migrations in sub-Saharan Africa (*Emu*, 100: 401–417) provides more detail on this topic.

Evolutionary consequences

Given why birds migrate, what are the evolutionary consequences? Migration might reduce the risk of extinction by allowing species to compensate for habitat shifts linked to long-term climate change, as well as discover novel habitat patches. However, migration might increase extinction risk through greater mortality associated with travelling through unfamiliar terrain and exposure to novel pathogens and predators (including specialists that prey on migrants, such as Sooty and Eleonora's falcons). Similarly, migration might promote speciation through the increased likelihood of vagrancy or the segregation of populations with different migration routes. But migration might also stifle speciation through enhanced gene flow.



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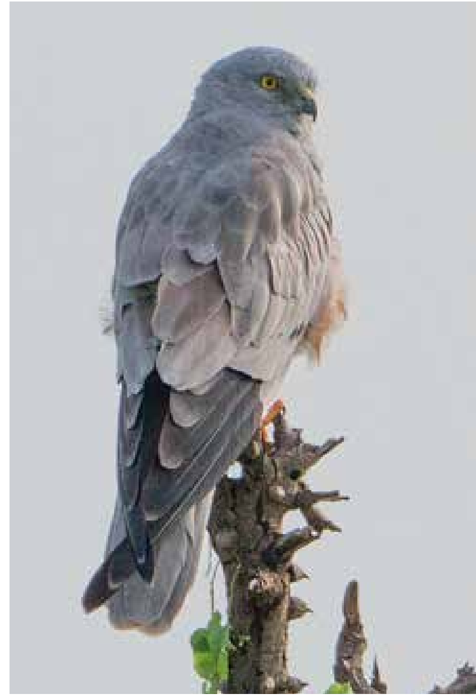
The Northern Wheatear's breeding range extends from north-eastern Canada and southern Greenland across northern Europe and Russia to Alaska, yet birds from all these areas winter in Africa. Canadian birds migrate more than 3000 kilometres across the North Atlantic to the UK, where they join European birds on their way south. Alaskan birds travel across the Bering Strait to Siberia, then through central Asia and the Middle East to reach Africa – more than 14 000 kilometres each way, which is particularly impressive for a bird weighing only 25 grams. It is unclear whether the failure to develop new wintering areas closer to these far-flung breeding sites results from a very recent range expansion or a lack of selection against such extreme migrations. Pectoral Sandpipers show the opposite pattern, with most of the Siberian breeding population wintering in the Americas.

A fascinating study by Jonathan Rolland and colleagues analysed patterns of migration among all birds (*Proceedings of the Royal Society B*, 281: 20140473). It concluded that the ancestors of birds were sedentary and that migration has evolved independently many times among birds. Historically, extinction rates of migrants have been substantially lower than sedentary species and their speciation rates marginally higher, resulting in a strong net advantage to migrants. This pattern was found across a range of speciose bird orders and has been detected in other bird groups. For example, the radiation of *Falco* falcons over the past five million years has been faster among lineages dominated by migrant species.

However, perhaps the most interesting finding from Rolland's paper was the marked difference in the mode of speciation among migrant and sedentary species. When non-migrants speciate, they typically split into two sedentary species; only rarely is one species migratory. Migrants can split into two migrant species as a result of adaptation to different routes (see box on Eurasian Blackcaps). The long-distance migrant shorebirds provide another interesting case study. Only five species regularly migrate to Africa, Australia and South America: Sanderling, Ruddy Turnstone, Grey Plover, Whimbrel and Pectoral Sandpiper. Many other shorebirds have Old and New World equivalent species, such as Common and Spotted sandpipers, Ringed and Semipalmated plovers, various stints, etc., suggesting that spatial segregation has led to



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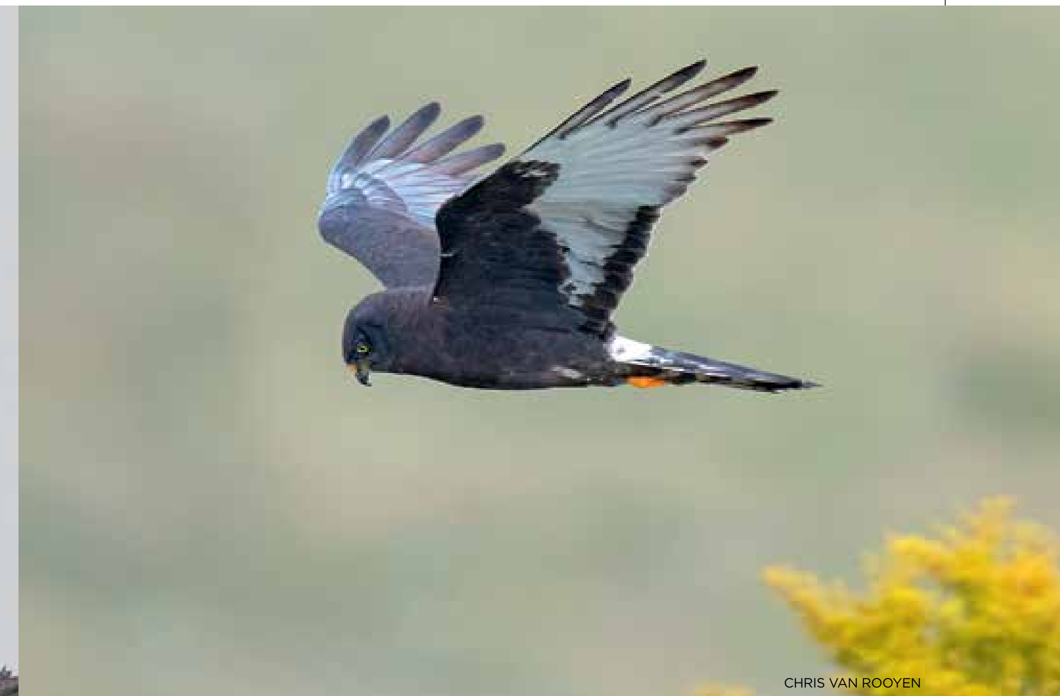

CHRIS VAN ROOYEN

Molecular studies of harrier evolutionary relationships have found close links between several north–south species pairs: Pallid (above, left) and Black (above, right) harriers, Western and African marsh harriers, Eastern Marsh and Swamp, Malagasy and Reunion harriers, and in the New World, Northern and Cinereous harriers (which required Northern Harrier to be split from the similar-looking Old World Hen Harrier). It seems plausible that the southern species evolved from migrants that settled in the south, diverging over time from their northern hemisphere ancestors.

speciation. However, this occurs less frequently than speciation among sedentary species, perhaps at least in part because of greater gene flow among migrant populations.

However, migrants also speciate by forming sedentary daughter species; this occurs much more often than when sedentary species split off a migratory species. Many species form when birds colonise isolated habitat patches, such as oceanic islands or forested mountain peaks, and the chances of such events are greater for migrant than sedentary birds, given their greater movements. A more interesting process is migration suspension, which occurs when some individuals start to breed in their traditional winter quarters, sometimes resulting in a new species.

Migration suspension

Migration suspension appears to have played a key role in the radiation of many migrant lineages. For example, the Black Harrier evolved from Pallid Harriers that settled in the south-western tip of Africa and other southern harriers probably evolved in the same way (see box above). Similarly, Antarctic Terns evolved from Arctic Terns that remained in their wintering grounds.

We can see all stages of migration suspension in southern Africa, from very occasional breeding by House Martins, through the faltering attempts to breed by White Storks and Leach's Storm Petrels, to well-established populations such as European Bee-eaters and Booted Eagles. The 'Cape buzzards' appear to be another example, arising from 'Steppe' Buzzards remaining to breed in the Western Cape. Possible hybridisation with resident Forest Buzzards just adds to the confusion – especially as Forest Buzzards probably evolved through a similar process in the past.

There have been few studies of how migration suspension occurs. The best example is the Barn Swallow, the world's most widespread swallow. Populations breed throughout much of Eurasia and North America and although some southern populations are sedentary, most winter in Africa, South America and Asia, even reaching northern Australia. A few birds occasionally overwinter in South Africa, but there are no breeding records. However, Barn Swallows started to breed in Argentina in the early 1980s and have since established a thriving breeding population.

To do so, they have changed their annual cycle to breed in the austral summer and moult in the austral winter. Like the European Bee-eaters that colonised South Africa in the 1850s, it was suspected that the southern breeders did not migrate all the way back to traditional breeding grounds, but rather wintered in the Neotropics. Initial >

European Bee-eaters only colonised South Africa as a breeding species in the 1850s. But like the Barn Swallows in Argentina, they have changed their annual cycle, arriving about one month earlier than northern-breeding migrants. The local breeding population is thought to winter in central Africa. They typically only start to moult their flight feathers after leaving South Africa, so birds in active wing moult are almost certain to be northern migrants.

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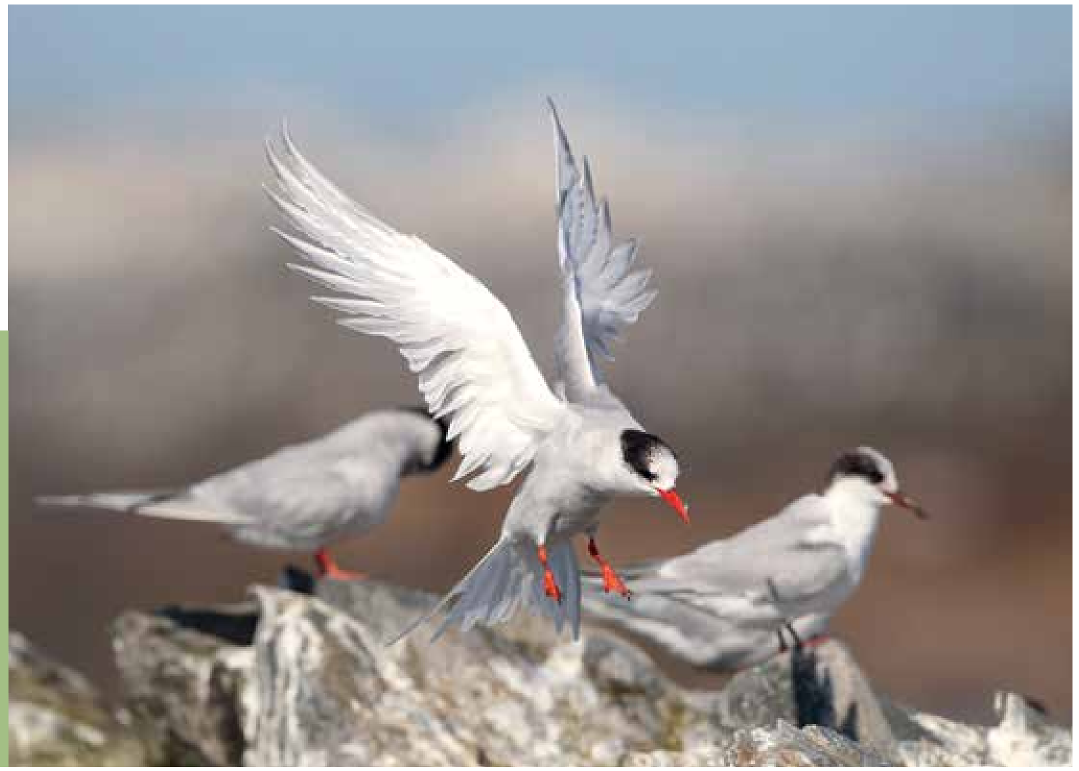
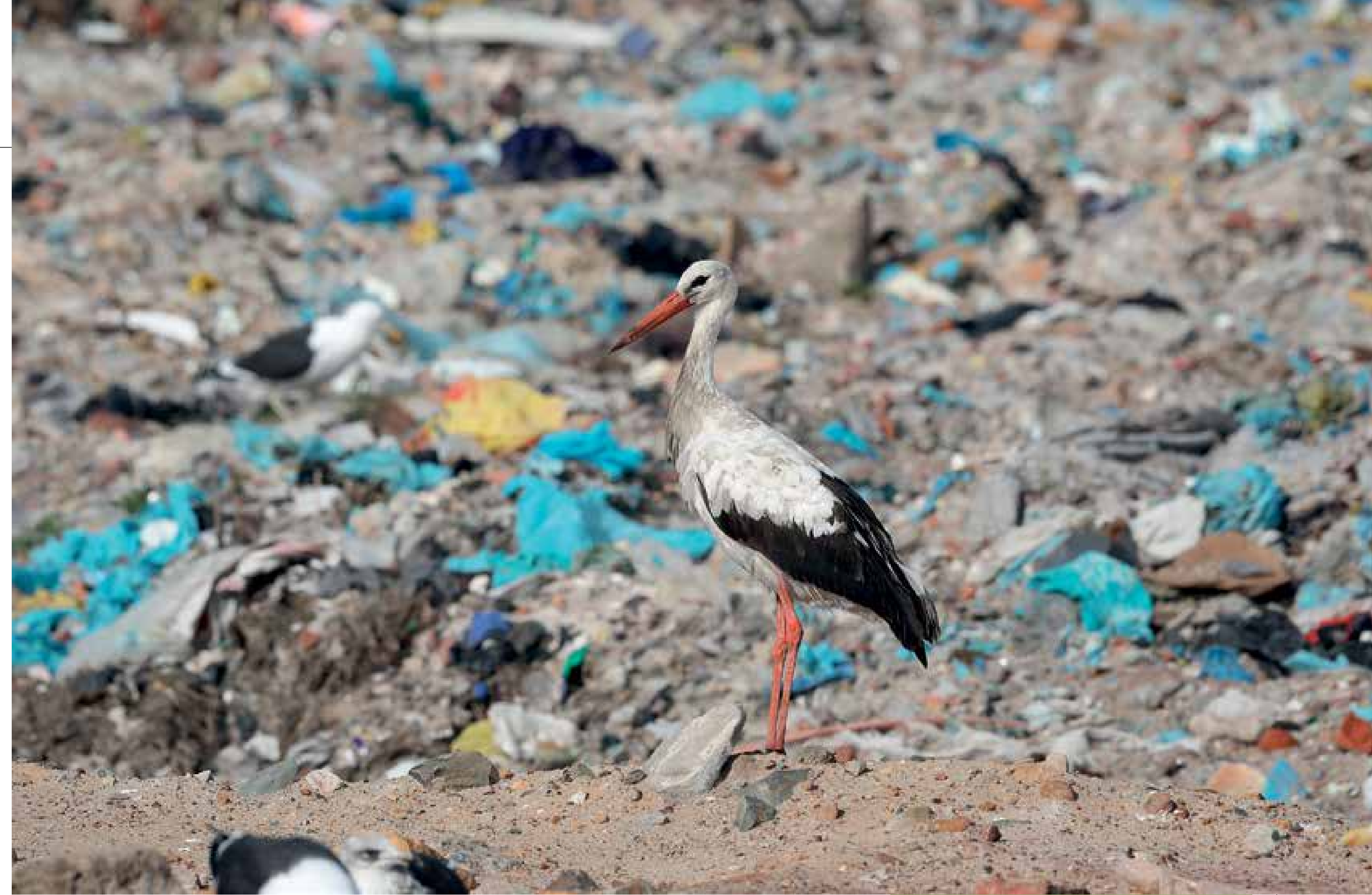
support for this hypothesis came from stable isotope studies of their feathers and it was recently confirmed by tracking nine birds from their Argentinian breeding sites to wintering areas in northern South America. They followed two migration routes; six travelled along the coast to near São Paulo before dispersing across Brazil, while three headed directly north through Paraguay to winter in western Amazonia. Their new migration routes are appreciably shorter than those of most North American Barn Swallows and avoid a challenging transit of the Gulf of Mexico or Caribbean Sea.

These swallows confirm that migration systems can be remarkably flexible and evolve within a few decades, despite the migratory urge being largely innate (see box on Eurasian Blackcaps). They have had to change not only the duration of migration, but crucially the direction. If young Barn Swallows reared in Argentina followed the genetic programming of their recent northern ancestors and flew south, they would end up in the ocean!



The Antarctic Tern's closest relative is the Arctic Tern and it is likely that they evolved from Arctic Terns that settled in the south. Among other seabirds, it is less clear in which direction the radiation occurred. Species such as gannets and fulmars are not trans-equatorial migrants and so it is more likely that a few stragglers that crossed the equator established new populations in the opposite hemisphere.



PETER RYAN (2)

The White Stork shows both a tendency to migration suspension, with small numbers breeding sporadically in South Africa, and increased residency in its main breeding range. Both changes result from human activities. South African breeders rely heavily on agricultural landscapes, especially lucerne fields, whereas in southern Europe resident birds make extensive use of scavenging at rubbish dumps – a practice that has also attracted flocks of storks to remain at dump sites around Cape Town.

Occasional reverse migration – where migrants go the wrong way – suggests that a simple mutation might be sufficient to change the direction of migration. In the case of the Barn Swallows, however, ongoing gene flow from new immigrants dilutes any local adaptations in the newly formed population. It seems more likely that environmental cues are sufficient to ensure most young swallows head north rather than south.

Quite what induces migrants to settle down and breed in their wintering grounds is unclear. There needs to be suitable habitat and much has been made of the role of bridges and other man-made structures as nesting sites for Barn Swallows in Argentina. However, similar structures occur throughout southern Africa and none has started to breed here. Other factors, including the diversity and abundance of similar species breeding in their wintering range, might also play a role.

Conservation implications

What does this mean for birds in a time of rapid global change? Although migration has tended to reduce extinction risk in the past, migrants are now more threatened than sedentary species. Several factors contribute to this problem. In an increasingly transformed world, migrants face ever more challenges during their epic flights, including colliding with structures such as buildings, power lines and wind turbines, and being dazzled by artificial lights at night. Migrants also require multiple areas to complete their life histories: breeding areas, wintering areas and often specific staging areas where they refuel during their journeys. Losing any one of these areas compromises their ability to survive. To make matters worse, migrants are harder to conserve because we have to protect many more areas to ensure their survival.

The good news is that many migrant species can rapidly adapt to changing conditions. This might result in increased residency in the core breeding area, or migration suspension and the establishment of new breeding populations in former wintering or staging areas. However, it is still not clear whether all bird species have this ability. If species exhibit little behavioural or evolutionary plasticity in migratory behaviour, they might be doomed to long-term population decreases. ◆