As the Starling Flies

by

Alice D. McBride

B.S. Biological Sciences
Cornell University, 2013

Submitted to the Program in Comparative Media Studies/Writing
in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE IN SCIENCE WRITING
at the
MASSACHUSETTS INSTITUTE OF TECHNOLOGY

September 2021

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Graduate Program in Science Writing
August 5, 2021

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ABSTRACT

The concept of science evokes forward momentum, a steady march of progress as scientists accumulate knowledge, refine hypotheses, and make theoretical leaps. But science, it turns out, can also meander as much as a wandering bird.

Illustrating this concept is research on the European starling, a migratory species whose annual travels have been helping shape the field of bird migration science for the past hundred and twenty years. Starling research, from early bird banding to current satellite tracking efforts, has been marked by moments of controversy and confusion alongside insight and discovery. Following starlings — and the researchers who study them — reveals the hidden twists and turns that characterize the path to scientific understanding.

Thesis Supervisor: Seth Mnookin
Title: Director, Graduate Program in Science Writing

Acknowledgments

In creating this thesis, I had a lot of help. I'd like to say thank you:

To Briana Abrahms, Thomas Alerstam, Stuart Bearhop, Letizia Campioni, Will Cresswell, Henk van der Jeugd, Matthew Kauffman, Roland Kays, Bart Kempenaers, Ellen Ketterson, Kevin Laland, Miriam Liedvogel, Thomas Oudman, Morrison Pot, Claire Teitelbaum, and Roswitha Wiltschko, for sharing your time and expertise with me.

To my cohort, Anna Blaustein, Robert Davis, Ali Gold, Elizabeth Gribkoff, Kelso Harper, Saima Sidik, and Nafisa Syed; to Tim De Chant and all the faculty and staff of the GPSW; to my housemates at Windsor; to Henry Cylkowski.

To Nathan Senner, Maria Stager, and Jelle Loonstra, for helping with networking, and to David Winkler and Theunis Piersma, for opening the door to field ecology. To Sophie Orzechowski and Elsie Shogren, always; to numerous field-crew friends; to the tree swallows, godwits, terns, and other creatures I've met along the way.

To my family members on both sides of the Atlantic, including Lee Downing, Caroline McBride, George McBride, Monique Verhoeven, and Oscar Verhoeven, with particular thanks to Mo Verhoeven and Abby McBride for heroic levels of support.

To my thesis advisor, Seth Mnookin. Thank you for helping me navigate every aspect of this thesis, and thanks especially for providing boundless encouragement.

As the Starling Flies:
Bird migration and the winding path of scientific discovery

A hint of noise punctuates the stillness of a clear autumn morning in 2018. It swells to a rustling whisper that fills the air, a quietly intense sound that seems to be everywhere, like a sudden rush of wind. Yet the shrubs and grasses that cling to the sandy dunes remain unmoved. As fast as it came, the sound fades into the distance.

The dunes seem deserted, the sound a mystery. But when it rushes in again a few minutes later, a glance to the skies reveals its source: a loose black cloud of birds, hundreds of European starlings, flying hell-for-leather down the Dutch coastline.

Flocks of starlings continue to fly past throughout the morning, coming from the northern reaches of the European subcontinent. Migrating southwest, the birds are funneled along the Dutch coastline as they head for wintering grounds in the Netherlands, France, Belgium, and the UK.

By late morning, the flocks are growing less cohesive, the starlings less intent on their journey. Small groups start to splinter off, flying inland, seeking a place to replenish their energy with food and rest. Little do they know what's in store — in the inland dunes, a Dutch biologist named Morrison Pot is lying in wait.

A lanky 28-year-old with dark hair and a friendly smile, Pot is hunkered down in a specially-built wooden shack set in a grassy clearing. In front of the shack, inconspicuous in the grass, a ten-meter-by-four-meter net is primed near a hidden speaker that plays whistling, warbling starling noises. A live starling — a compact, dark-feathered bird roughly the size and shape of a croissant — hops around in a cage next to the net. This inadvertent Judas was caught earlier in the day and set out as a decoy for his unsuspecting compatriots. "The trick is to lure them towards the nets," says Pot.

And it works. Overhead, a cluster of starlings headed inland check their flight. Convinced the site is a good spot to rest, they swoop down to land near the decoy starling. Pot watches intently as the birds drop into range. A yank of a rope, the sweep of the net — curving through the air like the page of a book being turned — and the trap is sprung.

Pot is studying migration, an aspect of the natural world that humans have been puzzling over for millennia. Roughly 40% of the world's birds, at least 4,000 species, are migratory. Early efforts to explain why huge numbers of birds seemed to disappear and then reappear every year led to theories that now seem ludicrous — birds transformed into a different species during the winter, or flew to the moon — but the difficulty of observing the behavior of an animal that simply wasn't there meant that far-fetched ideas persisted. Even Linnaeus claimed in 1758 that some birds spent the winter hibernating far underwater at the bottoms of lakes, though by that time most biologists thought such theories should be scrapped in favor of the idea that birds just move elsewhere for part of the year.

Even with scientists on the right track, there was plenty to puzzle over. "People knew virtually nothing about migration," says Henk van der Jeugd, head of the Dutch Centre for Avian Migration and Demography and one of Pot's research advisors. "They had no idea about where birds were coming from, where birds were going to." It was only with the advent of bird banding in the late 1800s that scientists were able to answer these fundamental questions and start understanding how migration works.

One of the most notable figures in the era of modern migration science was a Dutch biologist named Albert Perdeck. After World War II, he led a decades-long series of massive research projects during which he caught starlings in the Netherlands and released them in other parts of Europe. By manipulating the starlings' migratory routes, Perdeck illuminated fundamental components of migration, including the manner in which birds navigate to their distant destinations.

But over the past fifty years, some scientists have used Perdeck's research as proof of a different idea: that young birds have an instinctual sense of direction. That conclusion is controversial, partly because Perdeck's data doesn't explicitly support it, and partly because it plays into a familiar scientific debate — the concept of nature versus nurture, genetics versus environment. Is an animal's behavior hardwired into its genes, or learned through life experience?

Scientists are far from reaching a consensus about how much of a bird's migration behavior is innate. The quest to understand starling migration, begun by Perdeck and now continued by Pot, has the potential to help resolve that issue. At the same time, this unfolding story of starling research offers an intriguing window into the scientific process. As the influence of research experiments ripple forward through time, scientific knowledge — subject as it is to the interests and biases of its human executors — sometimes develops in meandering and unexpected ways.

Back in the Dutch dunes on that clear autumn day, Pot isn't thinking about the philosophy of science. By early afternoon, he and his colleagues have caught enough starlings for the day. They load up the car — the birds initially restless, then settling down in the dark confines of wooden boxes — and make the hour-long drive inland to the team's research facility at the Netherlands Institute of Ecology. "It's really cozy in the car with the birds," Pot says with a laugh.

At the research facility, the team unloads the wooden boxes and ferries them inside, where Pot will outfit each starling with a dummy satellite transmitter. These don't function, but look like the real thing: a flattened, inch-long rectangle with a solar panel, two antennas, and two loops of elastic which dangle from the casing. "It's really like a backpack," he says. "You just put the legs through these elastic bands."

Holding a starling in one hand, Pot stretches each elastic loop around one of the bird's legs and settles the dummy transmitter against its dark feathers, glossy with a green-and-purple metallic sheen. Pot gently spreads each wing out like a fan, checking that the tiny backpack doesn't impede the wing's range of motion. Then he releases the bird into a chicken-wire cage. A meter high and two meters across, it's big enough for five starlings to keep each other company and practice flapping around as they grow accustomed to their strange new loads.

Pot will spend the next day keeping an eye out to make sure his birds remain alert and healthy despite the added weight of the dummy transmitter and the stress of being captured. If all goes well, he'll soon begin the next phase of his project: catching another round of birds and outfitting them with fully functional satellite transmitters. Then Pot can track, in real-time, the travels of starlings as they migrate across the globe.

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Researchers in the present day use high-tech equipment like satellite transmitters to learn about birds as they migrate. But modern migration research got its start as a decidedly low-tech affair in the 1890s, when an enterprising schoolteacher in Denmark first devised a way to systematically track individual birds.

His method was straightforward: catch a bird, put a loose-fitting, engraved metal band around its leg, and then let it fly off again. “It was just a very simple idea,” says van der Jeugd. “Put a visible mark on the bird, and then hopefully someone will find it somewhere along the [migration] route.” The first successfully banded bird in 1890s Denmark, a starling, wore a band that read “VIBORG 1” — the name of the town, Viborg, and a number for the bird. People’s curiosity and a reliable postal service meant that when a bird wearing a band turned up later, whether it was caught in the garden next door or shot by a hunter hundreds of miles away, word would sometimes get back to the Danish schoolteacher.

“It was such a wonderful success,” says Thomas Alerstam, professor emeritus in evolutionary ecology at Lund University. “And it still goes on. Now millions and millions of birds are handled in banding schemes.” Today, there are researchers and bird enthusiasts all over the world who band birds and use online databases to report band sightings.

The data yielded by these little rings of metal give scientists insight into a bird’s movements — when and where the bird started, and when and where it ended up. Though banding can’t provide any information about the *route* a bird took between those start and endpoints, any glimpse into the inner workings of migration is valuable. Bird banding may have initially been driven by curiosity, but it’s now clear that understanding migration is crucial to conserving the world’s biodiversity and natural ecosystems.

“You're not going to be able to deal with managers or policy if you can't say how many birds there are and where they are, and how many are missing, and what lands need to be protected,” says Ellen Ketterson, distinguished professor of biology at Indiana University and founding director of the Environmental Resilience Institute. “[There are] three billion fewer birds in North America than there were in 1970. Where did they go?”

Migratory animals of all sorts are particularly vulnerable to both habitat destruction and climate change. They rely on multiple locations and specific habitats as they make their way across the globe, and changes to a single link in that chain can have serious consequences. Migrations are also timed to align with factors like seasonal temperatures and peaks in food availability — and many of these once-reliable rhythms are being disrupted by rapid global climate change.

“[Migratory birds] are universally declining,” says Will Cresswell, professor of biology at the University of St. Andrews. “They're between a rock and a hard place. Humans reduce habitat, but also increase climate change.”

I made my first foray into the world of bird migration as an undergraduate, when I took a summer job doing fieldwork for my university’s ornithology professor. I spent those hazy, hot months canoeing between bird-boxes mounted on posts in a pond, and observing, catching, banding, and measuring their feathered occupants. These were tree swallows — five-inch-long aerobatic wonders that fearlessly dive-bomb human invaders and subsist on flying insects that they snatch from mid-air. At the end of their breeding season, the tree swallows set off on a one-thousand-mile trip to their wintering grounds and I went back into the university lecture halls.

In field biology, as in life, one thing leads to another. Catching tree swallows on a pond in upstate New York eventually led me to the Netherlands, because Mo Verhoeven — my erstwhile canoeing partner, and eventual life partner — was starting a Ph.D. there. His project was on yet another migratory bird species, the black-tailed godwit. Built like long-legged Nerf footballs, these medium-sized shorebirds migrate between breeding grounds in the Netherlands and wintering grounds in southwestern Europe and western Africa. Mo's advisor was a well-known Dutch ornithologist named Theunis Piersma, who since 2004 has headed a large-scale project studying the biology of these godwits.

I joined Piersma's field crew and spent four springs immersed in the hands-on elements of migration research: searching for godwit nests in the Dutch meadows, putting bands on just-hatched chicks, trapping and banding their parents, and using a high-powered telescope to identify already-banded birds.

Meanwhile, Mo and a close colleague named Jelle Loonstra were investigating why individual godwits lead markedly different lives — some spend their winters in Morocco, others in Portugal; some migrate early, arriving in the Netherlands in the first frigid, dreary days of March, while others show up weeks later; some lay eggs early in the season, some late; some make their nest in the same place every year, others repeatedly move house. Mo and Jelle used satellite transmitters and other high-tech tracking devices to follow along, and this tracking data ultimately led them to conclude that learning plays a major role in a godwit's behavior.[1]

Through exposure to the work of Mo, Jelle, and Piersma, I started to realize that the question of nature versus nurture — a concept I had previously considered only in the abstract — was playing out right in front of me in the world of migratory bird research. It's an ongoing debate: How much of migration is dictated by genes and how much is shaped by external influences?

In 2020, Piersma, Mo, and Jelle joined forces with a behavioral ecologist named Thomas Oudman, who was doing postdoctoral research on migratory geese at the University of St. Andrews, to highlight what they felt were faulty assumptions about nature and nurture that had been widely incorporated into the field of migration science. To do so, they turned to a particular slice of migration history: Albert Perdeck's seminal research on starlings and the conclusions that have been drawn from it.

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Birds go, and they go far. The very earliest banding data confirmed this theory: gulls from Poland turned up in southern Italy, ducks banded in Scandinavia were found in Spain, storks from Denmark and Germany ended up at the southern tip of Africa. By the time Perdeck came around in the mid-1900s, researchers had moved beyond investigating *where* migrating birds went and were tackling the *hows* and *whys*. One fundamental question was how birds made their way across continents and oceans without getting lost — something that "puzzled people enormously," says van der Jeugd. "It's [still] one of the biggest questions in migration ecology."

Part of this puzzle was illuminated by studies in the 1930s and '40s that showed migrating birds could fly in a fixed direction — say, southwest — almost as if they were following a compass. True navigation, however, takes more than just a sense of direction: it takes a destination and an awareness of where

[1] I contributed to some of Mo and Jelle's scientific papers and was included as a co-author on several articles.

that destination is. Homing pigeons, famously, can find their nesting grounds regardless of where they start. Observations of banded birds hinted at the possibility that some migrating species were capable of performing the same navigational feat to find their wintering grounds.

Perdeck and his collaborators aimed to settle that question once and for all. They looked to the European starling, a species that flies south along the Dutch coast in enormous numbers every autumn. Already notable as the first species to wear engraved metal bands, the sleek little starlings were about to become the focal point of arguably the most ambitious migration experiments ever conducted.

Over the course of a decade, starting in the late 1940s, Perdeck and his team captured more than 11,000 starlings. Just as Morrison Pot would do seventy years later, Perdeck lurked in the dunes on the west coast of the Netherlands and trapped and banded migrating starlings. He released them in Switzerland, 400 miles away, and waited to see where they would end up. This process was repeated every autumn.

Waiting for the banding data to trickle in was a slow, gradual process. Banding, as a method, is hit or miss, and of all those thousands of captured starlings, only 354 turned up again later. But that was enough information for Perdeck to conclude that the starlings *did* use true, goal-based navigation while migrating.

Or at least the adult starlings did. The juveniles that Perdeck banded — young birds migrating for the first time — only managed to fly as if following an onboard compass.

On a map, these two different strategies play out in very different ways. Imagine walking down Fifth Avenue in New York, heading roughly southwest. Carry on in that direction long enough, and you'll eventually end up in the vicinity of Jacksonville, Florida — your intended destination in this hypothetical scenario. But if by some remarkable means — maybe a sudden cyclone — you're whirled away from Fifth Avenue and dumped into the streets of Detroit, what happens next? If you happened to be an adult starling, you would reorient yourself and head to Jacksonville. A juvenile starling, on the other hand, would just pick up as if it were still in New York…and end up in the middle of Mississippi, 500 miles off-course.

In Perdeck's real-life displacement experiments, the adult starlings reoriented and made their way northwest from Switzerland to find their usual wintering grounds. The juveniles, meanwhile, went southwest and ended up in the wrong parts of Europe. This discrepancy between adults and juveniles added an intriguing twist: How much of migratory behavior is learned through experience, and how much of it is hardwired into an animal from the start?

On the one hand, Perdeck's experiments showed that at some point in their lives, starlings learn to navigate: They go from only being able to fly in a fixed direction to also being able to reorient toward a goal. "There's no doubt that those patterns are there," says Bart Kempenaers, research director of the Max Planck Institute for Ornithology. But in the 1970s, two decades after Perdeck first published his research on displaced starlings, the interpretation of those patterns moved onto shaky ground. Instead of simply concluding that starlings learn navigation, researchers began routinely citing Perdeck's work to support the idea that juvenile starlings start out with an innate sense of direction.

It seems like a reasonable notion. Perdeck's research showed that juvenile starlings, plunked down in unfamiliar territory and left to fend for themselves, fly off in what would normally be considered the correct direction. Doesn't that prove they have an innate sense of direction?

Not necessarily, it turns out.

Along with Piersma and his godwit team, Oudman argues that the juvenile starlings' behavior could have been due to any number of other factors. "Researchers don't really give it a lot of thought when…they think about the different options of developing migration behavior," says Oudman. Maybe juveniles learned to fly southwest by following adults on their way down the Dutch coastline before Perdeck caught and displaced them to Switzerland. Or perhaps, after being displaced, the juveniles chose their direction based on environmental cues *in* Switzerland. Whatever the reason, Perdeck's study was only designed to figure out *how* starlings behaved, not *why* they behaved that way.

In 2020, Piersma and Oudman's group published an article in the *Journal of Avian Biology* to express their concern that Perdeck's displacement experiments had been wrongly interpreted (and then wrongly cited and re-cited) as proof of an innate sense of direction in starlings. "They want to remind people that 'innate' is too simple a way to understand the development of behavior," says Ketterson.

But reaching a more complex understanding of migration behavior requires technology that's more sophisticated than bird banding.

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Every field of science changes over time, and the study of bird migration has been both marked and shaped by a series of revolutionary techniques. New methods and technologies — from banding birds, to developing better binoculars, to sequencing DNA — have enabled researchers to, in Alerstam's words, "see new worlds."

How researchers track migrating birds is a case in point. From metal bands, bird tracking leaped into the high-tech realm during World War II: radar, it turned out, didn't just pick up enemy aircraft. It showed bird flocks and individuals, too. "At close range, you could identify them," says Alerstam, noting that different types of birds are distinguishable by the pattern of their wingbeats. By catching birds mid-flight, radar gave researchers their first glimpse into the actual process of migration — a brief window into altitude, speed, direction.

From there, tracking techniques have become more and more advanced. As technologies like GPS came into play, researchers started attaching high-tech tracking devices directly to their study subjects — everything from caribou to cuckoos to crocodiles. By periodically recording their geographic position, devices like these create a trail of digital breadcrumbs. Connecting those dots can reveal the route a specific animal takes. "You almost get to know it, and how it handles its life," says Alerstam.

Different types of tracking devices have specific advantages. For example, geolocators have tiny batteries that can last for years and in total weigh less than a paperclip, which means even very small birds can carry them. They measure longitude and latitude by recording sunlight levels, much like the mariners of an earlier age. "You get the time of day that the sun rose and the sun set, and then you figure out where the animal was," says Roland Kays, a zoologist at North Carolina State University and the North Carolina Museum of Natural Sciences.

But light-level data can only provide a general location, and sometimes the data points are completely uninformative: sunlight patterns during the equinoxes and in the vicinity of the equator don't always yield a geographic fix. Perhaps most limiting, though, is the fact that geolocators only store data — they don't transmit it. "You have to hope and pray that your bird shows up again in the same place a year later so you can catch them and get [the geolocator] back," says Kays.

Satellite transmitters, in contrast, can pinpoint location to within a few meters with as little as a few minutes between each geographic fix. They send their data to an online database, so researchers need only step over to a computer to find out where their tech-toting animals are.

Easy-to-access, accurate, real-time location data from a specific animal is every migration researcher's dream. "In the Perdeck study you needed to translocate an awful lot of starlings, thousands of individuals, to get a few data points," says Kempenaers. "With the tracking technology nowadays, you can see everything." Even satellite transmitters have their limitations, though. Until very recently, a single transmitter cost several thousand dollars, with additional fees for the privilege of using the satellite network. But from the start, the biggest constraint to using satellite transmitters — at least when it comes to putting them on birds — has been their weight.

The earliest satellite transmitters, used in the 1990s, were clunky affairs that weighed nearly half a pound. The first bird species to carry one was the wandering albatross, a ghostly white giant with an 11-foot wingspan. For a 22-pound albatross, a half-pound transmitter is roughly 2% of its total body weight. This may not sound like much, but it's the equivalent of strapping a two-liter bottle of soda to a 190-pound person and making them carry it around everywhere they go — including on periodic ultramarathons. Put much more weight on a migratory bird, and the energetic cost starts to impede the animal's ability to go about its business of migrating, reproducing, and surviving.

This weight issue initially limited satellite tracking to larger bird species. But electronic components have shrunk over the years, and so have the transmitters. "While the whole of this process has advanced, you could use it for smaller and smaller animals," says Alerstam. The most cutting-edge satellite transmitters now weigh only a few grams — and this miniaturized technology is the reason that Morrison Pot was hanging out in the dunes of the Netherlands trying to lure starlings to his nets.

Pot wants to leverage the ongoing technological revolution to repeat and build on Albert Perdeck's starling displacement experiments from seventy years ago. "For the first time, we are able to track starlings," says Pot. "It's a nice opportunity to redo this experiment and learn so much more." He's catching juvenile and adult starlings in the same nook of the Dutch coastline, at the same time of year, and will displace them the same way Perdeck did. But using satellite transmitters will unlock far more information about migration than Perdeck was able to gather even with his army of thousands of banded starlings. "[Perdeck's data] only has a release location, and then a location where [each] bird was found," says Pot. "We will know what happens in between."

The satellite transmitters Pot is using weigh only four grams, which is lighter than a sheet of standard computer paper. Newly developed by the International Cooperation for Animal Research Using Space — ICARUS, for short — these transmitters, which cost between $500 and $600, are part of a larger vision meant to take the next forward leap in migration research. By generating a mountain of new tracking data, making it publicly available, and treating the whole effort as a massive collaboration, ICARUS hopes to create an “internet of animals” that will enable biologists and conservationists to study and monitor the pulse of the living Earth in a cohesive way.

Pot is one of the first researchers to try out the ICARUS system. In staging a high-tech encore of Perdeck’s experiments, he’s aiming to strap these transmitters onto 100 starlings per year for three years. If all goes well, Pot’s starlings will go on to yield a wealth of data about their migratory behavior, revealing the *details* of the routes they take and the ways in which displacement affects their migration.

But Pot’s research has the potential to do even more — by shedding new light on the learned elements of starling migration, and adding nuance to a scientific conversation about the relative importance of learning in animal behavior. “We don't know what drives the migratory heading of these juveniles,” he says. “We really hope to build on this result of Perdeck, and find out how these juveniles migrate.” If there is indeed more to juvenile starling migration than just built-in instinct, there’s a good chance Pot’s tracking data will show it.

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These stories about bird migration — how we learn about it, and the disagreements and difficulties that arise in the process — bring to light a conundrum that plagues science in general.

There are two options as a scientist, according to Cresswell. You can read the scientific literature and immerse yourself in existing knowledge before thinking about the next scientific step. Or you can skip the existing knowledge, and just think about the next step. “Second option...you’re going to be wasting your time,” says Cresswell. Clearly, it doesn’t make sense to start from scratch. “First option, well...then you’re just following all the other idiots.” But flippancy aside, isn’t that how science works?

For better or worse, scientists operate within a culture of existing ideas. In each field of science, certain ideas are taken for granted or thought to be impossible, certain patterns jump out more readily from a dataset, certain elements are chosen to explore in the next study. “We have conceptual frameworks which channel our thinking in particular directions,” says Kevin Laland, professor of behavioral and evolutionary biology at the University of St. Andrews.

The field of bird migration is no exception. Migration is an overwhelming subject to study, thanks to the many habitats and resources birds rely upon *en route*, the physical adaptations that have evolved to enable birds to make their journeys, the varied behaviors, the careful timing. It makes sense for researchers to hone in on a small piece of this interwoven tapestry and follow the threads as best they can. But the elements researchers choose to scrutinize, and the methods they employ, have an outsized influence on the conceptual framework that shapes the field.

Take, for instance, the debate about learned versus innate migration behavior. In influential experiments starting in the mid-twentieth century, researchers studied captive birds in controlled environments. They observed the behavior of these captives during the times of year the birds would normally be migrating. Over the years, such studies yielded fundamental discoveries about migration — for example, that birds are capable of orienting by the stars and can sense the magnetic field that surrounds the Earth.

These controlled experiments cut out complex variables and were powerful and informative in their simplicity. But they were limited for the same reason. “By keeping the environment [controlled] to establish a point," says Ketterson, "the environment is also sterile, uncomplicated, and short on information that might modify [the captive birds'] behavior."

Studying migration in this way — with captive birds kept from the external world's influences, in some cases from the moment they hatch — was a prime opportunity to think about the role of genetics. But these studies were not designed to evaluate the role of the environment in shaping actual migration behavior in the wild. This disparity in genetic versus environmental focus was folded into the conceptual framework underlying migration research.

"I think the importance of innate [processes] probably has been slightly overstated as a consequence of this early work," says Stuart Bearhop, professor of animal ecology at the University of Exeter. For example, he says, "people have almost dismissed the possibility of social exchange," the idea that animals exchange information, which is one way the environment can influence their behavior.

This is part of a bigger pattern in science in which the role of genetics is given disproportional weight in research efforts. "Once people have identified a genetic cause," says Laland, "it actually discourages them from investigating other potential causal influences." But the reverse doesn't happen, he continues. "If people identify learning as playing *a* role in migratory behavior, they don't jump to the conclusion 'Therefore, there is no role for genes in that migratory behavior.'"

What happened with Perdeck and his starling studies shows how much influence a conceptual framework can have. For decades, data on starling navigation have been used to bolster the idea of innate migration behavior. In the wake of the recent paper by Piersma and Oudman's group, other scientists have acknowledged that alternative explanations, including learning, should have been considered all along. "In that sense, there is no disagreement," says Oudman. "But I do think there's a big disagreement in what people think will be the outcome [of further study]." He suspects that some scientists are still prone to underestimating learning because of the unbalanced framework in which they were trained.

That scientific fields sometimes get stuck in certain modes of thinking isn't surprising. But it does mean that part of a scientist's role should be to actively try to identify the boundaries of the framework they operate in — by keeping an open mind and open lines of communication, to start. "People in other fields think differently. They have different intuitions, they have different starting assumptions," says Laland. "They'll come along and say, 'Well, why do you think that? Surely *this* might be the real cause.'"

Collaborating across fields is one way to keep science moving forward. And advances in technology — like little bird backpacks that communicate with satellites — can reveal other holes in an existing conceptual framework. "I think we can be sure that the more things we try, the more remarkable things we are going to find out," says Bearhop.

If Albert Perdeck could see the starling research of the present day, he would probably agree. It will soon be known what starlings and their satellite transmitters can reveal about the mysteries of bird migration — but as for the mark that will make on the scientific field, only time will tell.

Bibliography

Interviews and correspondence:

Abrahms, Briana. Assistant Professor, University of Washington, Seattle, WA. Zoom interview: January 20, 2021.

Alerstam, Thomas. Professor Emeritus, Lund University, Lund, Sweden. Zoom interview: February 23, 2021.

Bearhop, Stuart. Professor, University of Exeter, Penryn, UK. Zoom interview: January 21, 2021.

Campioni, Letizia. Postdoctoral Researcher, ISPA University (Instituto Universitário de Ciências Psicológicas, Sociais e da Vida), Lisbon, Portugal. Zoom interview: January 23, 2021.

Cresswell, Will. Professor, University of St. Andrews, St. Andrews, UK. Zoom interview: December 16, 2020.

van der Jeugd, Henk. Director, Dutch Centre for Avian Migration and Demography, Wageningen, The Netherlands. Zoom interview: March 4, 2021.

Kauffman, Matthew. Associate Professor, University of Wyoming, Laramie, WY. Zoom interview: February 17, 2021.

Kays, Roland. Research Associate Professor, North Carolina State University, Raleigh, NC. Phone interview: February 25, 2021.

Kempenaers, Bart. Research Director, Max Planck Institute for Ornithology, Seewiesen, Germany. Zoom interview: January 15, 2021.

Ketterson, Ellen. Distinguished Professor, Indiana University, Bloomington, IN. Email correspondence: February 9, 2021. Zoom interview: February 23, 2021.

Laland, Kevin. Professor, University of St. Andrews, St. Andrews, UK. Zoom interview: March 19, 2021.

Liedvogel, Miriam. Research Group Leader, Max Planck Institute for Evolutionary Biology, Plön, Germany. Zoom interview: January 19, 2021.

Oudman, Thomas. Postdoctoral Researcher, University of St. Andrews, St. Andrews, UK. Zoom interviews: October 27, 2020; March 2, 2021.

Pot, Morrison. Ph.D. Candidate, Netherlands Institute of Ecology, Wageningen, The Netherlands. Zoom interviews: October 29, 2020; January 25, 2021; June 17, 2021.

Teitelbaum, Claire. Ph.D. Candidate, University of Georgia, Athens, GA. Zoom interview: January 19, 2021.

Wiltschko, Roswitha. Adjunct Professor (retired), Goethe University, Frankfurt, Germany. Email correspondence: January 9, 2021. Zoom interview: January 11, 2021.

Additional research:

Alerstam, Thomas, and Anders Hedenström. "The Development of Bird Migration Theory." *Journal of Avian Biology* 29, no. 4 (December 1998): 343. https://doi.org/10.2307/3677155.

Bateson, Patrick. "Taking the Stink out of Instinct." In *Alas, Poor Darwin: Arguments Against Evolutionary Psychology*, edited by Hilary Rose and Steven Rose. New York: Harmony Books, 2000.

Cole, Leon J. "The Tagging of Wild Birds: Report of Progress in 1909." *The Auk* 27, no. 2 (April 1910): 153–68.

Cresswell, Will. "Migratory Connectivity of Palaearctic-African Migratory Birds and Their Responses to Environmental Change: The Serial Residency Hypothesis." *Ibis* 156, no. 3 (July 2014): 493–510. https://doi.org/10.1111/ibi.12168.

Jouventin, Pierre, and Henri Weimerskirch. "Satellite Tracking of Wandering Albatrosses." *Nature* 343, no. 6260 (February 1990): 746–48. https://doi.org/10.1038/343746a0.

Laland, Kevin N., and Steven Rose. "Sir Patrick Bateson FRS. 31 March 1938–1 August 2017." *Biographical Memoirs of Fellows of the Royal Society* 66 (June 2019): 25–51. https://doi.org/10.1098/rsbm.2018.0040.

Lincoln, Frederick C. "Migration of Birds." U.S. Fish and Wildlife Service Circular 16. Washington: United States Government Printing Office, 1998.

Lincoln, Frederick C. "Notes and News: Hans Christian Cornelius Mortensen." *The Auk* 39, no. 4 (October 1922): 592. https://doi.org/10.2307/4073617.

Lincoln, Frederick C. "Some Results of Bird Banding in Europe." *The Auk* 42, no. 3 (July 1925): 358–88. https://doi.org/10.2307/4074382.

Lincoln, Frederick C. "The History and Purposes of Bird Banding." *The Auk* 38, no. 2 (April 1921): 217–28. https://doi.org/10.2307/4073884.

Lisovski, Simeon, Silke Bauer, Martins Briedis, Sarah C. Davidson, Kiran L. Dhanjal-Adams, Michael T. Hallworth, Julia Karagicheva, et al. "Light-level Geolocator Analyses: A User's Guide." *Journal of Animal Ecology* 89, no. 1 (January 2020): 221–36. https://doi.org/10.1111/1365-2656.13036.

Pegan, Teresa M., David P. Craig, Eric R. Gulson-Castillo, Richard M. Gabrielson, Wayne Bezner Kerr, Robert MacCurdy, Steven P. Powell, and David W. Winkler. "Solar-Powered Radio Tags Reveal Patterns of Post-Fledging Site Visitation in Adult and Juvenile Tree Swallows *Tachycineta bicolor*." *PLOS ONE* 13, no. 11 (November 2018): e0206258. https://doi.org/10.1371/journal.pone.0206258.

Perdeck, Albert C. "An Experiment on the Ending of Autumn Migration in Starlings." *Ardea* 52, no. 3–4 (December 1964): 133–39.

Perdeck, Albert C. “An Experiment on the Orientation of Juvenile Starlings during Spring Migration.” *Ardea* 62, no. 3–4 (1974): 190–95.

Perdeck, Albert C. “An Experiment on the Orientation of Juvenile Starlings during Spring Migration: An Addendum.” *Ardea* 71, no. 2 (1983): 255.

Perdeck, Albert C. “Bird-Ringing in Europe.” *Endeavour* 6, no. 1 (January 1982): 27–33. https://doi.org/10.1016/0160-9327(82)90007-2.

Perdeck, Albert C. “Orientation of Starlings after Displacement to Spain.” *Ardea* 55, no. 3–4 (1967): 194–202.

Perdeck, Albert C. “The Starling as a Passage Migrant in Holland.” *Bird Study* 14, no. 3 (September 1967): 129–52. https://doi.org/10.1080/00063656709476158.

Perdeck, Albert C. “Two Types of Orientation in Migrating Starlings, *Sturnus vulgaris* L., and Chaffinches, *Fringilla coelebs* L., as Revealed by Displacement Experiments.” *Ardea* 46, no. 1–2 (August 1958): 1–37.

Piersma, Theunis, A. H. Jelle Loonstra, Mo A. Verhoeven, and Thomas Oudman. “Rethinking Classic Starling Displacement Experiments: Evidence for Innate or for Learned Migratory Directions?” *Journal of Avian Biology* 51, no. 5 (May 2020): jav.02337. https://doi.org/10.1111/jav.02337.

Preuss, Niels O. “Hans Christian Cornelius Mortensen: Aspects of His Life and of the History of Bird Ringing.” *Ardea* 89, no. 1 (2001): 1–6.

Underhill, Les G., Anthony J. Tree, H. Dieter Oschadleus, and Vincent Parker. “Review of Ring Recoveries of Waterbirds in Southern Africa.” Cape Town: Avian Demography Unit, University of Cape Town, 1999.

Verhoeven, Mo A., and A. H. Jelle Loonstra. “On the Behaviour and Ecology of the Black-tailed Godwit.” Ph.D. Thesis, University of Groningen, Groningen, The Netherlands, 2020.

Wiltschko, Roswitha, and Wolfgang Wiltschko. “Avian Navigation: A Combination of Innate and Learned Mechanisms.” In *Advances in the Study of Behavior*, 47: 229–310, 2015.