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Common Cuckoos *Cuculus canorus* belong to the species-rich Cuculidae, the single family in the order Cuculiformes (Payne & Christie 2016). Compared with other birds, Cuckoos are very much in a league of their own, and many of them are brood parasites (Davies 2000). Several of them are also migratory, sometimes over long distances and over open oceans. This has led to persistent bepuzzlement about the ways in which they develop their individual migrations. When a bird does not grow up with its own parents, not even in a nest of its own species but in that of an alien host, as is the case for Common Cuckoos, nobody can teach them, right? They are supposed to migrate alone (Newton 2008), flying at night (Thorup *et al.* 2020). So, during migration they have no other option than to rely on inherited directional information (Newton 2008), do they?

Recognizing that some migratory birds such as cranes (Gruidae) travel in family groups and thus learn the routes from experienced adults (Mueller *et al.* 2013, Abrahms *et al.* 2021), Common Cuckoos have become the primary example of the opposite, a species migrating under strict genetic instruction (Vega *et al.* 2106, Thorup *et al.* 2020). In that line of thinking, an interesting displacement study with adult Common Cuckoos was actually *based* on the proposition that “migrating birds follow innate species-specific migration programs capable of guiding them along complex spatial-temporal routes” (Willemoes *et al.* 2015). This paper then confirmed itself with the concluding statement that “the cuckoos possess spatial knowledge far beyond their population-specific flyway scale.” Not ‘just’ a population specific route would be inherited, but a concept of a much larger area.

Which brings us to 1 June 2020, corona-time. During a rare and precious get together of part of our lab-group, Roeland Bom, Eva Kok and myself have lunch in our garden in Gaast, northern Netherlands. We are discussing Common Cuckoos and ask ourselves whether they really always fly alone. What is the empirical evidence? Could they migrate in loose flocks, but that this has not been observed? Exactly then, at 13:15 p.m., we hear Cuckoos, and an instant later two birds, probably males, fly overhead at a height of about 80 m calling “cuckoo, cuckoo”. They call continuously and are followed at a short distance by a smaller bird which we think is a female. They wander off in a southern direction. Suddenly, there they were, Cuckoos in a small flock in plain air, an exciting illustration of possibilities just discussed.

That there would be an interspecific gradient, from learning the migratory routes (with experienced family or flock members as teachers) to relying on genetic information alone, with ‘socially-informed’ species like Whooping Cranes *Grus americana* at one end of the gradient and ‘genetically-instructed’ species like Common Cuckoos at the other, assumes two things. (1) There exists a dichotomy between genetic information on the one hand, and information of all other kinds on the other (this is the familiar ‘nature vs. nurture’ dichotomy). (2) The sources of information guiding a young and naïve individual migratory bird during its first migration are different in *essential* ways between species. I propose that both assumptions are untenable.

Decades ago, theoretical biologists, spearheaded by Susan Oyama (Oyama 1985, 2000, Oyama *et al.* 2000), pointed out that the dichotomy that puts genes (‘nature’) against everything else (i.e. the environment, ironically called ‘nurture’ rather than ‘nature’!), is just one way to divide up the many possible ‘developmental resources’ shaping a phenotype. They also pointed out that this dichotomy is unlikely the most heuristically productive (Oyama *et al.* 2000). A ‘developmental resource’ may be anything that influences the development of an organism, varying from cues, favourable or unfavourable growth conditions, and includes instructions of a memetic or a genetic nature. Thus, developmental resources encompass the genes, the maternal and paternal proteins, including various levels of hormones, in an egg, the permeability of the egg-shell and what comes through, the shape and temperature and smell of the nest, the other local environmental conditions (in many dimensions) experienced during the first few weeks of life, and so it goes on. Clearly, genes are just one among hundreds or thousands of such resources, and there is no argument why genes as a resource should be privileged (Oyama *et al.* 2000). This destroys the first postulation. That the second assumption is also untenable follows from the appreciation that any ontogeny represents a continuous interaction between processes in a developing organism and the myriad developmental resources, the precise nature of the interactions varying all along the developmental trajectory (Oyama 1985). A richness of interactions amongst a multitude of developmental resources should occur in all developing organisms, even Common Cuckoos.

In this light it is unfortunate, and scientifically unproductive, that most students of bird migration (for résumes see, e.g. Berthold 2001, Liedvogel *et al.* 2011, Flack *et al.* 2022) have bowed to privileging genes as the main developmental resource, of course acknowledging carefully that environmental influences kick in too – at some stage. At the risk of sounding cartoonesque, this is basically the view exposed in a keynote address by the geneticist Sydney Brenner in 1982 – at a symposium commemorating the 100th anniversary of Charles Darwin's death: given the complete DNA sequence of an organism and a large enough computer it would be possible to compute that organism. I take this anecdote from Richard C. Lewontin's foreword to the 2001 revised edition of Oyama (1985). Whereas Brenner expected it to happen 'soon', such a computation of an organism still has to materialize 40 years later.

Let me explain why this continuing absence of a computed organism is actually expected, by citing Lewontin a bit more: "Genes 'do' nothing, they 'make' nothing… DNA is among the most inert and nonreactive of organic molecules: that is why stretches of DNA can be recovered intact from fossils long after all the proteins have been lost." Of course, genes are a crucial developmental resource. Without DNA there would be nothing for the cell machinery to take its instructions from to assemble proteins. Without genes there would be no development, but without all the other developmental resources there would be no development either. Young Cuckoos start building and continue fine-tuning an image of the world from the moment they hatch, probably even from conception. They are likely to integrate a multitude of cues and make individually varied decisions in response to those cues. Common Cuckoos are amazingly complex developmental systems that cannot be reduced to a product of genetic instruction alone.

Well then, how dó fledgling Common Cuckoos find their way to a distant and rather specific parts of the African continent, some individuals doing so even after being displaced as young birds? We know they will, as today we can even follow them online during their travels from northwest Europe to Central Africa, and back, year after year (www.bto.org/our-science/projects/cuckoo-tracking-project; Hewson *et al.* 2016). In a study in which juvenile and adult Common Cuckoos were displaced 1800 km eastward just before the start of southward migration, Thorup *et al.* (2020) found that the displaced juveniles left the area of release a bit earlier than the adults. In this experiment birds were extracted from their known world and dropped into a new one, and it is quite possible that displaced young birds would generally be faster to take cues (e.g. from experienced local adults) than the displaced adults who had gone further in integrating one or more years of memorized information across space and time.

One alternative narrative to the current common one is that young Common Cuckoos actually are not the lonely voyagers that they are portrayed to be. In such a narrative, young cuckoos are conscious observers of the world around them, taking cues even while perching in a tree somewhere (Davies 2015). Cuckoos could be thought of as birds developing their migratory decisions and actions with reference to more knowledgeable birds, other Common Cuckoos or other species carrying out similar migrations at similar times (Cohen & Stattersfield 2020). In this narrative, the description of a northward passage of large numbers of Common Cuckoos through the East African savannah springs to relevance. Although individual Cuckoos kept some distance to each other, this migration was described as a very social phenomenon (Prins 1986). Migrating at night, even if not carried out in the dense structured flocks that characterize waders and geese (Piersma *et al.* 1990, Kölzsch *et al.* 2020), Common Cuckoos may still exchange information and take cues from each other, or from other species. Even though the average adult may migrate ahead of the average juvenile, in an exciting tracking study the two age groups showed remarkable overlap in the timing of their southward migration (Vega *et al.* 2016).

Male Cuckoo flying overhead (photo Wilfred Marissen, Zuid-Holland, 3 June 2011).

To sum up, it is difficult to see how Common Cuckoos are fundamentally different from the shorebirds that I am familiar with, Black-tailed Godwits *Limosa limosa*, for example. In these Godwits, the young of the year do not travel with their parents and on average they migrate later than the adults (Verhoeven *et al.* 2022), just like Common Cuckoos. Nevertheless, all our observations are consistent with the idea that the development of their migratory routines relies on the accumulation of experiences including forms of learning (e.g. Loonstra *et al.* 2019, Verhoeven *et al.* 2022).

The time has come, for migration biologists and indeed the biological community at large, to abandon the DNA-as-blueprint dream of Sydney Brenner, accept and embody the criticisms of that DNA-centric world by Dick Lewontin (2000) and embrace the rich thinking on organisms as developmental systems developed by Susan Oyama and others. Granting ourselves the freedom to think about multiple developmental causes during a time that we can track individual birds, young and old, with uncanny precision over much of their lifetimes, should bring migration ecology to the forefront of evolutionary biology. Think about what this could mean to advance our understanding of animal responses to global change! There is intellectual work to be done.

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