

What if Charles Darwin had stopped over in Africa?

by

Michel LOUETTE

KEYWORDS. – Darwin; Birds; Africa; Evolution; Variation within species.

SUMMARY. - Charles Darwin based his famous evolution proposals extensively on bird observations. When still a young man, at home in England, he studied behavior in the peacock and variation in the domestic pigeon. Some years later, following his voyage with the Beagle, he studied the variation in the island populations of Galápagos birds.

In this review I discuss potential bird study subjects from the Canary Islands, the Comoros and mainland Africa, regarding Darwin's findings:

- Communication in birds
- Variation in domesticated birds. The pigeon as a study subject, in comparison to another potential candidate: the canary
- Variation in wild birds
- Evolution and natural selection as shown by conspecifics on islands: Galapagos finches, in comparison to potential candidates on circum-african archipelago's
- Sexual selection as shown by the peacock, in comparison to the Congo Peafowl
- Divergence in the vocalizations of birds on islands
- Apparent exceptions to Darwin's findings, such as colorful females in some birds

Numbers in brackets [] refer to the notes, p. xx

Introduction

The review starts from two sources. Firstly, I briefly outline how, almost two centuries ago, Charles Darwin (1809-1882) brought about a revolution in thinking in biology, especially by introducing the concept of evolution by natural selection. Many of Darwin's findings have subsequently been confirmed by later researchers. I have focused on the birds he studied, and which formed the basis of his findings. Secondly, I speculate whether his results could have been obtained with birds from Africa, a continent that Darwin did not (or hardly) know and where I was able to conduct a number of studies myself.

From an early age, Darwin was making observations in his environment in England and experimenting with domesticated animals, especially the pigeon, because he was very fond of this bird. He became famous after he had made the sea voyage on the Beagle. The ship departed in 1831 and circum-navigated the globe, so Darwin found many opportunities to note the variety of creatures he

observed, particularly among the unique animals of the Galápagos islands. Upon his return home in 1836, he published a series of books, resulting from the notebooks and diaries during his voyage, beginning with the narrative of the voyage (Darwin, 1839). His later work, essential reading for scientists, historians, and anyone with an interest in the natural world contained the conclusions (Darwin, 1859, 1871). This was based mainly on his field observations, supplemented with the study of ornithological specimens collected during the Beagle voyage (Steinheimer, 2004). With the exception of this long cruise, Darwin, it is believed, never left Great Britain (Richardson, 1916). Although the Beagle called at ports in circum-African islands (the Cape Verdes and Mauritius) and Cape Town, Darwin was unable to make enough observations in Africa for his evolutionary concepts. He had wanted to visit Tenerife in the Canaries for a year, but a cholera quarantine forced the Beagle to pass without stopping. Many scientific developments have been influenced by chance, and the idea that Darwin might have come to similar conclusions on the basis of African studies is worth investigating. I will here discuss suitable bird examples from Africa known at present and compare them with Darwin's studies.

Communication in birds

Birds need to communicate. They do it to a certain extent vocally (I will come back to this later) but mostly visually, observing beautiful feathers and their form and sometimes colored bare skin. In the following discussion other body language aspects (such as evaluation of size, strength, fighting spirit and possession of weapons such as spurs on pheasant cocks) are not addressed.

A uniform plumage is useful for recognizing a bird's own species [1]. There are many sexually monomorphic [2] birds. But this strategy can be less efficient: a lack of difference might hinder the recognition of the sex, because visual cues are often used in courtship. However, a *caveat*: human vision often fails to distinguish sexual difference among supposedly monomorphic birds, such as e.g. the Blue Tit *Cyanistes caeruleus* (fig. 1) (Eaton, 2005). It does occur in England, so Darwin must have known it, and may have wondered about the reason for its sexual similarity. Thanks to recent technology, it becomes clear what the birds themselves see: the plumage of male and female Blue Tits is different under UV-light (birds can see UV)!

For the other species, those with dissimilar feathering, quite often, the female is cryptically [3] patterned, and the male is not. But in a number of such bird species, surprisingly, the female, although wearing a rather different plumage, does not look particularly cryptic. But beware of rapid conclusions! Among the birds with quite different sexual plumage figures the European Blackbird *Turdus merula*, familiar to Darwin (shown on fig. 2, together with several congeneric species of the genus [1] *Turdus*). One would agree that the brownish female is cryptic (for inconspicuousness while breeding), and the entirely black male is not. However, Tomiałojć & Bursell (2006) show that the male would still be cryptic in forest, the native habitat. Unlike the European Blackbird, the sexes in some other thrush species on fig. 2 look identical to the human eye. So, even among relatives, the plumage patterns vary to a great extent.

Important color zones can be present in other parts of the body (not just the feathers). Prum & Torres (2003) investigated color of skin, bill, tarsus [4], and toes from 17 families [1] of birds from around the world. Judging from the phylogeny [5], the necessary mechanism of pigment production has evolved separately more than 50 times. To give one example, just as in some domestic pigeon breeds, in several wild birds, the circumorbital skin developed to a quite substantial fleshy and very bright protuberance, or 'eye-wattle' [6] which also serves a communication function. These eye-wattles exist in several members of the African genus *Platysteira* (fig. 3) (Louette, 2006). Their sexual difference concerns the plumage color of the throat: in the illustrated species (Black-throated Wattle-eye *Platysteira peltata*) black in the male and brown in the female, whereas the eye-wattles are

nearly identical. The related species of the genus *Batis* (fig. 4) lack eye-wattles. Here, an important communication signal is the bright iris of the eye (in most species it is deep yellow; in some it is red or orange according to sex, such as here in the male of the Cape Batis *Batis capensis*). The Iris color serves as a species recognition tool where it is sympatric [7] with other, yellow-eyed species.

Researchers often use color in birds to study evolutionary processes. The existence of beautiful feathering in males (which was acquired over evolutionary time through selection) has been explained by others, since Darwin. The extravagance of certain male decorative elements in particular has attracted the attention of scholars. Prum (2017) published a groundbreaking book; he challenges Darwin's "really dangerous idea" of aesthetic evolution by mate choice. He defines this process as the evolution of a communication signal through sensory/cognitive evaluation. He thinks that beauty can perhaps sometimes be the result of chance and not necessarily of evolutionary adaptation. So, in his view, preference of females for aesthetics may not (necessarily) be related to fitness. How these conclusions fit in the communication need of all the bird species has not yet been completely elucidated. Let us also emphasize that the bright feathers of females (which occur in a limited number of species) have received less attention by scientists.

Variation in domesticated birds

Darwin studied several domesticated birds as descendants of single wild bird species, including chickens *Gallus gallus*, peafowl *Pavo cristatus*, Canary *Serinus canaria* and pigeon *Columba livia*.

The domestic pigeon

Secord (1981) discusses at length the special bond Darwin had with the pigeon. Darwin realized that the different breeds, although descended from one species, arose through human selection, which was possible thanks to the variation that had occurred in the original wild bird. The wild Rock pigeon is native to southern Eurasia and was domesticated at several times and places. Archeological evidence points to human use as early as the Pleistocene. In Europe, the popularity of the pigeon hobby rose markedly in the 17th Century, after several breeds with characteristics different from the wild phenotype were imported from the Middle East (Shapiro & Dormian, 2013). Not only color variation is involved (including eye color and increased eye-wattle size and color), but also e.g., general size, behavioral aspects, particular body position, unusual or even abnormal feather characteristics (frilled feathers, crest, feathered legs, extra feathers in the tail) and increased size of the nose wattles. All these aspects are the (exaggerated) results of domestication; they are related to body language in the pigeon.

What if Darwin had studied the canary nowadays?

The wild Canary was imported into Europe from the Canary Islands in the late 14th century because of its remarkable song. The process of domestication by which the wild type was transformed by selection into a pure yellow one occurred centuries ago (Birkhead et al., 2004). The many canary breeds consist nowadays of three groups: stature canaries (bred for their peculiar

shape), color canaries and song canaries. In Darwin's time, selection had already taken place; so, shape variation already existed but color variation in the canary breeds was much more restricted than nowadays. For example, it is only more recently, in 1930, that the artificial hybridization of canaries with the Red Siskin *Spinus cucullatus* introduced the factor "red" (Perez-Beato, 2008).

Cardoso et al. (2023) have shown that canaries are excellent candidates as a model to investigate the genomics [8] of evolutionarily relevant traits. Also, communication and mate choice behavior are promising study subjects, using the canary. In his day, however, Darwin would have learned less than what he observed in the domestic pigeon, for which the multitude of breeds already existed since

times immemorial and were available in England. Many Canary breeds were imported there only later. But the study of vocalizations in the canary could have helped him in making his conclusions.

Variation within the species in wild birds

Variants in the plumage occur in approximately 3.5 % of bird species. Raptors account for a disproportionately high number. The genus *Buteo* has more polymorphic [2] species than any other raptor genus: 15 out of 25 (Galeotti et al., 2003). Some studies suggest that variation is useful for a predator because potential prey does not easily form a picture of the threat. These polymorphisms are interesting from an evolutionary perspective because they are heritable and therefore provide a good model for understanding mechanisms. The occurrence of variation provides the opportunity for selection and therefore for evolution. It is considered the ultimate reason for the emergence of new species. The 'struggle for life' that is always present does the rest; through natural selection, certain individuals have the most offspring, because they have acquired innovative characteristics from the variation that allow this. This process is a key mechanism of evolution and is at the origin of the expression "the survival of the fittest" (Darwin, 1859).

Spectacular polymorphic species of birds are known from tropical mainland Africa. I (Louette, 2006) collected material on remarkable variation in males of the Yellow-bellied Wattle-eye *Platysteira concreta*: this bird has a yellow-bellied variant [2] and a red-bellied variant (fig. 5), and this is not necessarily related to sexual difference. There is no explanation for this yet; both variants seem equally fit.

Another case of variation in plumage occurs within the species in paradise flycatchers *Terpsiphone* in Africa and in Madagascar. The variant males are either whitish or reddish, as for example in the Malagasy Paradise Flycatcher *Terpsiphone mutata* (fig. 6 A and 6 B). I will come back to that species later.

Darwin did not study an obvious color polymorphism among Galápagos birds, namely the one in the Red-footed Booby *Sula sula*. It is considered one of the most spectacular polymorphic seabirds with three adult plumage variants: white, white-tailed brown and brown (Baião & Parker, 2008). Darwin also was not aware that members of the Geospizidae do show color polymorphism in the nestlings, with beaks either pink or yellow (Enbody et al., 2021), because this required a level of field observation that he was not used to do; he limited himself mainly to collecting specimens.

Evolution and natural selection

Darwin's study on the Galápagos

There are more than 20 species in the now aptly named Darwin's finches of the family Geospizidae, each with a distinctive beak form. Darwin already saw that, although obviously related to each other, many had developed adaptations that make them better suited to their particular environment. Darwin's finches are a prime example of adaptive radiation. We now know that all were derived from a common ancestor, but each occupies an ecological niche to which it is adapted, principally because of the size and shape of the beak, in relation to the food (Grant & Grant, 2002). Estimating the structure of the evolutionary tree has become possible because of studies on DNA sequence variation [8] among them.

Among the other animals on the archipelago of the Galápagos that provoked Darwin's thoughts are of course the giant tortoises, but to limit ourselves here to the birds, in fact he, before anything else, noted the diversification of the Galápagos mockingbirds (genus *Nesomimus*), leading to his initial concept of adaptive radiation. With molecular study, it was later possible to confirm the monophyly [5] of the mockingbird representatives on all the islands, suggesting a single colonization of the

archipelago, followed by diversification (Arbogast et al., 2006), as also shown for the Darwin's finches.

Below, I will discuss what Darwin could have learnt from the birds that colonized and diversified on islands in circum-african archipelago's (Canary Islands and Comoros), which he did not visit.

Darwin's study on the peacock

The Indian peafowl *Pavo cristatus* ('peacock' or 'Indian peacock') gives a well-documented example of the principles of evolution. One of Darwin's major ornithological subjects, it was (and still is) living in many courtyards in England commensally with man and can be considered as domesticated (there are e.g. white variants). The male's excessively long upper tail coverts named "train" (not the tail feathers themselves) catch attention (fig. 7). The females are a dull version of the male (and without the train). From times immemorial, man was wondering how the species was able to survive in its native range in southern Asia, a land with tigers *Panthera tigris* and leopards *Panthera pardus* while carrying such a long and heavy attribute which makes it difficult to escape predators. This feature bothered Darwin, who wrote in 1859, "the sight of a feather in a peacock's tail...makes me sick!" (Dahlin, 2018). In those early days, in fact, Darwin doubted that the peacock's train did support his theory of evolution; he believed that such an elaborate feature would be a disadvantage because it was burdensome.

Darwin saw "female choice" in Indian peahens, which prefer to mate with cocks that have the largest, most elaborate trains. He discusses this in detail in his later book (1871). He then speculated that the peacock evolved its exotic train to attract a mate, thus helping it increase the number of offspring. In fact, the idea that organisms with favorable traits are more likely to reproduce and thus pass those traits on to their offspring seemed unlikely to Darwin's contemporaries. But it has been credibly explained by later scientists. The development of extravagant secondary sex characteristics [10] makes a male animal more attractive to a female. If over the generations the females select these traits, they can develop to extremes over time – at which point they hinder rather than help survival. Darwin's argument suggests that animals possess a sophisticated ability to judge the attractiveness of each potential mate and the quality of his genes against a sort of checklist of criteria. So, Darwin, in addition to discussing natural selection, introduces the concept of sexual selection [11].

Could Darwin's sexual selection findings have been discovered in Africa?

There are quite a number of male birds with excessive plumage features. These males belong often to species that operate in "leks" [12]. Prum (2017) found spectacular examples from South America and especially New-Guinea. Lekking exists in some Phasianidae, and, in Africa, a famous member lives: the Congo peafowl *Afropavo congensis* [13] (fig. 8). Molecular research [8] has shown that the two bird genera *Pavo* and *Afropavo* are each other's closest relatives (Kimball et al., 1997). However, they are quite different in appearance (the male Congo peafowl 'Congo peacock' does not possess a train) and in their breeding behavior; the Congo peacock takes care of the chicks (Van Bemmelen, 1961). Also, unlike the two Asian species, the Congo peacock, although it is often seen in small groups (fig. 8 A), may in fact be monogamous (Louette & Mulotwa, 2022). This is suggested by the feathering: blue in the male; brown in the female; the two sexes have many dorsal feathers with metallic edges (see fig. 8 B). Worldwide, in many birds with highly colorful males, the females also have some or quite extensive bright coloration, even showing iridescent 'metallic' feathers, but in most species, the pattern is a poor derivative of that of the males, and far from the extent it has in the Congo peahen. Congo peafowl habitat is primary forest, but old secondary forest adjacent to primary forest is also used as a foraging area (Mulotwa et al., 2010). The male Indian peacock has difficulty flying with its

long train, but lives in largely open areas; does the different morphology in the Congo peafowl permit a life in closed forests, and can we assume that a very long tail would be a nuisance? One can also learn from this that kinship in nature does not imply a closely similar way of life.

Nevertheless, Darwin would have been able to find a lekking bird in Africa, although he would have needed to travel far: the polygynous [12] Jackson's widowbird *Euplectes jacksoni* of East African grassland, studied by Andersson (1992). Each male displays on his own display court: a cleared circular track around a grass tuft. The male performs a jump display that attracts females, and a ground display directed at visiting females. Breeding males are black with a tail 20 cm long, which is conspicuously exhibited during display. Females and non-breeding males are streaky brown with a short tail. Tail length was the single most important predictor of male mating success, suggesting that the tail is a cue for female mate choice. The rate of visits by females was correlated with male copulatory success. To put it simply: the results suggest that female Jackson's widowbirds prefer males with long tails.

Another example and well-studied group with males possessing excessive long tails are the already mentioned paradise flycatchers of the genus *Terpsiphone* (fig. 6). Paradise flycatchers do not have a lek mating system, but males often invade each other's territories, and the females sometimes have extra-pair copulations with these invaders (preferably with longer-tailed males?) (Mizuta, 2000).

Could Darwin's evolutionary findings have developed from other islands?

Oceanic islands are excellent systems for allowing biologists to evaluate evolutionary hypotheses due to their relative simplicity of habitats, potential of replicated study design and animal populations with conspicuous variation in form, color and behavior. For birds, there are two especially spectacular radiations on archipelagos. The Galápagos islands that Darwin called at (merely by chance) and the Hawaiian Islands. The radiation in other archipelagos are quite unspectacular in comparison. For the circum-African islands, the Gulf of Guinea islands and the Seychelles are really poor in replicas of related landbirds on the different constituent islands. The Canary Islands and the Comoros are better off; they have proved a useful subject for evolutionary ornithologists who seek to unravel how biodiversity arises and disappears. Both archipelagos have existed for millions of years, but it is unclear when sufficient permanent vegetation became available. This is the all-important factor to enable land birds to survive.

Canary Islands

The Canary Islands are a group of seven islands situated in the Atlantic Ocean close to the northern part of the African continent. As in many other oceanic islands, their flora and fauna are characterized by many endemics. The most likely sources for colonization are the Iberian Peninsula and North Africa. Not only are these the closest continents, but also present-day prevailing winds and sea currents suggest them to be the source areas. Altogether five extant endemic bird species and 30 endemic subspecies [1] have been described. The Blue Tit (fig. 1) occurs on all the islands with recognizable populations on each, based on sound and body measurements. The present classification groups the birds of Tenerife, Gran Canaria and La Gomera in one cluster, and the birds from Fuerteventura and Lanzarote in another, while the two remaining islands, La Palma and El Hierro have separately recognizable populations (Kvist et al., 2005). There are just subtle differences in color. Dietzen et al., (2008) noted the most most variable morphological parameters among the populations: bill width and the distance of bill tip to nostril. Thus, one could indeed speak of an initiation of differentiation for ecological reasons. The morphological differences among island populations of the Blue Tits on the Canary Islands are however much less pronounced than e.g. among Darwin's finches on the Galápagos.

Comoros

The Comoro Islands are a group of four islands situated in the Indian Ocean between the African (Mozambique) coast and Madagascar.

The variants in color in the Malagasy flycatcher were mentioned above. Madagascar is the origin of the populations on the four islands of the Comoros (Bristol et al., 2013). The changes in plumage that occurred after these colonizations are remarkable. Males of some of these small island populations are monomorphic (white males do not exist there) and some have much shorter tails. On Grand Comoro, furthermore, birds have developed a velvet cap on the head (fig. 6 C), which is missing elsewhere, even in Madagascar (Louette et al., 2008). This is an innovative development in the design within the species. In addition, on the Mascarenes, independently colonized from Madagascar, the plumage has evolved to a remarkable colorless drab state.

Another example: one population of Frances's Sparrowhawk *Accipiter francesiae* lives on Madagascar, while three of the Comoro Islands each have distinct subspecies. The plumages of these four populations are peculiar. This raptor has a dimorphic plumage for the male and female in Madagascar (rather unbarred white ventrally in the male, but banded brown in the female). This is not the case on the Comoros. While on Mayotte (fig. 9 A) both sexes wear feminine [9] plumage (resembling the female on Madagascar), in Anjouan and Grand Comoro (fig. 9 B) the situation is the opposite; there, both sexes wear a masculine [9] plumage (resembling the male on Madagascar). So, dimorphic plumage is evidently not essential for mate recognition. These sparrowhawks show major differences between islands in density and habitat preference. On Mayotte, the density is very high. Maybe this becomes possible because of less aggression between the birds that wear all a feminine plumage, although females are larger and socially dominant. On Anjouan and on Grand Comoro the density is only about 10 % of the one on Mayotte (but this could be the result of human influence). Molecular analysis indicates that each of the three Comoro islands was colonized from Madagascar in the same historical period, geologically speaking relatively recently. This indicates rapid, divergent morphological and ecological evolution of the small insular populations (Louette et al., 2011). Is sexually recognizable plumage under such circumstances no longer necessary? And why has it evolved in opposite directions on the islands?

Bird vocalizations

Darwin (1871) was the first to propose a causal association between sexual selection by female preference and the evolution of what he called 'instrumental music' in birds. Bird song is generally associated with males. In fact, both males and females sing in numerous species, but vocal performance in females has been little studied. A well-known case is the European robin *Erithacus rubecula* (fig. 10 A), a species with a distinctive color pattern, present in both sexes. The individuals on the European breeding grounds are, however, different ones from the ones occurring there later in the year. European robins also sing in autumn and winter to defend exclusive individual territories, but the females present in spring do not do so. Darwin was fully aware of this fact (see a letter from J. J. Weir - 18 May 1868 in: Darwin Correspondence Project, "Letter no. 6181"). During winter, plasma levels of testosterone are elevated in females, but not in spring (Kriner & Schwabl, 2010); of course, Darwin did not have this information. Let us turn now to Africa. Voelker et al. (2017) describe vocalizations of the remarkably similar looking African relatives in the genus *Stiphornis* (fig. 10 B). These birds are also sexually monomorphic and signal bright color on the breast (also in females) for the necessary aggression to achieve territory defense. The researchers were unable to confirm possible differences in sound between the sexes in this genus.

Acoustic characteristics were also studied in dull-colored birds, but, all these years after Darwin, the living world did not reveal all its secrets. An underexposed aspect is the variation between closely related, albeit isolated populations, such as on islands; on the Comoro islands our team investigated this, using the tape recorder and sound analysis. The three island subspecies of the Comoro Thrush *Turdus bewsheri* are rather dull colored with limited plumage difference between the islands). This is a rather simple situation, resulting from a colonization by a stock from Africa (the genus *Turdus* does not occur in Madagascar, see Voelker et al., 2007). The Anjouan subspecies is illustrated on [fig. 11](#). This thrush is not shown on fig. 2. The vocalizations differ very clearly between the birds of the three islands (Herremans, 1988).

A more complex acoustic differentiation in the same area exists in the genus *Nesillas*, dull-colored warblers. *Nesillas* occurs in Madagascar, with 'offshoots' on Aldabra and the three westernmost Comoros (with two species on Moheli) (Louette et al., 1988). We suggested a relationship from the acoustic data: the species on Grand Comoro and the smaller of the two sympatric [7] ones on Moheli are ancient colonists of western Madagascar stock. Birds on Aldabra also belong to this cluster [5]. These all have complex calls. By contrast, the warbler of Anjouan may be an ancient offshoot of the taxon of eastern and northern Madagascar. The larger of the two species on Moheli is a secondary, more recent offshoot. The latter three taxa utter calls which are simple in structure. Fuchs et al. (2016) confirmed the complex colonization history of this group, using DNA. Because of these technologies, in his day, Darwin would have been unable to unravel such situations.

Apparent contradictions to Darwin's conclusions

Darwin (1871) developed the thesis that females, not males compete for access to mates in some species. In other words, these are 'sex role reversed' regarding mating competition and sexual selection, compared to most birds. Over the ensuing 150 years, studies of the reversed sex role stimulated an important conceptual breakthrough (Fritzsche et al., 2021). This has led to a richer and more nuanced understanding of animal mating systems and to a proper appreciation of the fundamental role both sexes play in shaping these systems.

Among the few bird species that have reversed the parental duties (where the males take on the duties of brooding the eggs and raising the young) there are several African representatives that I will not enumerate in this short review. And indeed, in those cases, the female is more beautifully feathered and/or larger than the male. One can argue that this reversion of the beautiful plumage to the other sex 'proves' indirectly the existence of sexual selection in 'normal' birds. Remember also the already mentioned bird species with a similar plumage pattern in males and females, but with quite different color patterns. In Africa, this is illustrated by members of the family Platysteiridae (see the black breast band in the male and the brown breast band in the female of the Cape Batis, fig. 4), a bird that lives near Cape Town, where the Beagle called briefly. Darwin commented on geology and collected some beetles, but did not study birds there. In Darwin's day, ornaments occurring in females received less attention and were considered as nonadaptive, correlated effects of selection on males. However, recent studies suggest that female ornaments may have evolved quite independently of male showiness. New models predict that both male mate choice and female contest competition will occur under certain circumstances. Thus, selection acting on females might be a widespread cause of female ornaments (Amundsen, 2000).

I made some observations on the family Platysteiridae that relate to these phenomena (Louette, 2005). All 30 species have colorful feathering in both sexes, in many species with typical dimorphism [2] (black patches in males, replaced by brown in females such as those in fig. 3 and fig. 4). Atypical (masculine) females, and even a 'semi-masculine' female exist in some, such as in fig. 5, according to the general color pattern. Likewise, one species displays an atypical (feminine) male, but its female is

'hyperfeminine' [9], and still another has a typical female and a 'semi-feminine' [9] male. Relationships of these atypical plumages with habitat, small range, small number of individuals and high local density need to be better explored. Possibly, much of the plumage variation, but not all, can be linked to ecological variation. I noticed that a masculine female does occur in those species that live in low densities or on mountain tops (fragmented habitat). There, territorial behavior may be limited. The feminine male does occur in species that live at high densities high densities (which could possibly suppress aggressive behavior; or is the first a consequence of the other?). To compare: as mentioned above, Louette et al., (2011) found a feminine male for Frances's Sparrowhawk living in high density on Mayotte. These cases correspond most likely to restricted distributions and therefore in a situation with restricted genetic exchange.

There is also an ongoing debate concerning sex recognition and the reason for a specific female plumage. Price (2019) considers that differences in colors and songs may have evolved in a number of cases through losses in females rather than gains in males. Some of these characteristics tend to be associated nowadays with life history traits other than mating systems. They may be due to other factors, such as seasonal migration or territorial behavior. Altogether, these recent findings support the view that sexual dimorphism is an evolutionary byproduct of multiple, different selection pressures acting on both males and females. Johnson et al., (2013) declare bluntly "when males are bright and females are dull, one should not immediately assume that this is the result of sexual selection in males". The studies as yet do not include examples from Africa. In any case, Darwin would have raised his eyebrows!

ACKNOWLEDGEMENTS

The author is most grateful to Kasper Berg, Sergio Maria Bianchi, Nik Borrow, Teresa Hart, Raphael Jordan, Alexis Lours and Claire Spottiswoode, who provided photos directly. Other photos were obtained from the Cornell Lab of Ornithology/Macaulay Library, with the help of Deborah Cipolla-Dennis and Vanessa Powell from the following photographers: Tony Doty, Olivier Langrand, Allison Miller, Nathalie Santa Maria, Alan Van Norman and Daniel Winzeler. Alec Luro permitted the use of a figure from his paper and Isabelle Gerard (Royal Museum for Central Africa, Tervuren) was helpful with the permission for others.

Through their pointed and constructive criticism, two anonymous reviewers allowed me to improve my manuscript. I thank them for that.

NOTES

[1] According to the Linnean system in biology, a species is the unit in nature. For the convenience of researchers, species have since a long time been partitioned into geographical subspecies, and species can be grouped to the next level: genus. Genera can be grouped in a family. Nowadays, these splits and groupings are often based on molecular research.

[2] Polymorphism: individuals showing different morphological characteristics (often conspicuous colour differences), whereas monomorphic species share the same characters. Monomorphism: all individuals showing just one feather color. Dimorphism: individuals showing two feather colors. Variant: a group of individuals with a particular plumage type.

[3] Crypsis: the ability of an organism to conceal itself by having a color, pattern, and/or shape that allows it to blend into the surrounding environment.

[4] Tarsus, more exactly tarsometatarsus: the "lower leg" of birds. This bone is equivalent to a fusion of the mammalian ankle and foot bones.

[5] Phylogeny: the science of studying the evolutionary history of organisms. Monophyly: belonging to the same phylogenetic stem. Cluster: a group of related species or subspecies.

[6] Circumorbital: around the eye. Wattle: protuberance resembling horns on the sides of the head. They can be expanded considerably when the birds are excited or wounded.

[7] Sympatry: the occurrence of different species in the same area.

[8] Genomics: the study of the complete set of genes (the genome) of organisms; there are nowadays methods to study the DNA sequence. This molecular research enables the construction of evolutionary history, something Darwin was completely unaware of.

[9] Masculine: looking like a male, even if biologically definitely of the female sex. Feminine: looking like a female, even if biologically definitely of the male sex. I use also the derivatives 'hyperfeminine' (more female characteristics than usual) and 'semifeminine' (with certain female characteristics, but not all).

[10] Secondary sex characteristic: a physical characteristic of an organism that is related to or derived from its sex, but not directly part of its reproductive system. For birds, e.g. colorful plumage and distinctive song.

[11] Sexual selection: the process that males compete with other males for access to females, while females choose the most attractive males to bond with. Both mechanisms help explain how the species evolved over time.

[12] Lek: The (often traditional) site where males assemble, display, and court females mates. These males are often polygynous: they mate will mate with several females, given the opportunity.

[13] The Congo peafowl was only described in 1936. its discovery was one of the most sensational ornithological events of the 20th century, because of its possible relationship to the Asian peafowls *Pavo*. Congo peafowl do not thrive in captivity and are as yet not domesticated, in contrast to of their Asian relatives.

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List of illustrations and the legends.

Fig. 1. – Blue Tit *Cyanistes caeruleus* (photo by Sergio Maria Bianchi on Tenerife, Canary Islands).

Fig. 2. – Males and females of many *Turdus* species and their geographical location. The color scale indicates the number of species with overlapping breeding ranges. Illustration from *Journal of Evolutionary Biology* (Luro & Hauber, 2022).

Fig. 3. – Black-throated Wattle-eye *Platysteira peltata*. A: male. B: female (photos by Claire Spottiswoode in Royal Museum for Central Africa collection).

Fig. 4. – Cape Batis *Batis capensis*. Female to the left, male to the right (photo by Tony Doty).

Fig. 5. – Variants Yellow-bellied Wattle-eye *Platysteira concreta*. A: yellow-bellied (photo by Nik Borrow in Cameroon). B: red-bellied (photo by Raphael Jordan in Côte d'Ivoire).

Fig. 6. – Madagascar Paradise Flycatcher *Terpsiphone mutata*. A: male white variant from Madagascar (photo by Alan Van Norman). B: male red variant from Grand Comoro (photo by Kasper Berg). C: female from Grand Comoro (photo by Allison Miller).

Fig. 7. – Indian Peafowl *Pavo cristatus*. Male parade with a deployed train and an attentive female (photo by Daniel Winzeler in Sri Lanka).

Fig. 8. – Congo Peafowl *Afropavo congensis*. A: group composed of the two sexes: males glossy blue, female shining brown. B: members of the same group, in excitement (photos courtesy of Teresa Hart, taken with camera trap in DR Congo).

Fig. 9. – Frances's Sparrowhawk *Accipiter francesiae*. A: feminine bird on Mayotte (photo by Nathalie Santa Maria). B: masculine bird on Anjouan (photo by Olivier Langrand).

Fig. 10. – A: European Robin *Erithacus rubecula* (photo by Alexis Lours in France). B: African Forest Robin *Stiphrornis erythrothorax* (photo by Nik Borrow in Uganda).

Fig 11. – Comoro Thrush *Turdus bewsheri* on Anjouan (photo by Kasper Berg).