

Review

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Review

Birds: Did Evolution of Biological Novelties Compromise Their Capacity of Effectively Adapting to Extreme Environmental Conditions?

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Simple Summary

Among the extant air-breathing vertebrates, birds are the most species-rich animal group. Together with other traits, morphologically, physiologically and behaviorally, they are exceptionally well-adapted for life under diverse ecological habitats. To various extents, most species of birds are presently enduring the effects of extreme environmental conditions which among others are causing drastic biodiversity changes, population declines, shrinking of ecological ranges and extinctions. Here, a critical appraisal of the exceptional adaptive specialisations of birds; the most important adverse environmental conditions which birds are facing now and; the biological after-effects of their living under the severe surroundings are documented and explained. It is suggested that under the existing threats from the current environmental conditions of which climate change and habitat devastation and pollution are the foremost ones, generally, the adaptive capacities of birds appear to have weakened. Since the environmental conditions are progressively worsening, it is suggested that conservation of especially the most adversely affected species of birds is urgently warranted.

Abstract

Foremost, the structural-, functional- and behavioural traits of birds relate directly or indirectly to powered flight, an elite mode of locomotion which has importantly made them what they are - 'specialist and extreme animals'. Placing them at the pinnacle of the evolutionary hierarchy, birds possess exceptional biological specialisations which have conferred profound survival advantages. The adaptive novelties of birds are particularly exhibited by the exemplary morphological and physiological refinements of their respiratory system, the lung-air sac system. To contribute to the ongoing discussions and debates on the impacts of the existing extreme environmental conditions (ECs) on the biology of birds, here, a perspective is posed that the adaptive specialisations which birds acquired ostensibly under different ECs may have undermined their capacity of efficiently adjusting to different ones. To explain the viewpoint, the following aspects are considered: the specialist- and extreme biology of birds; the prevailing harsh ECs which are brutally impacting on birds and; the consequences from their enduring the harsh conditions which include among others global warming and habitat devastation. It is contended that under the existential threats, the adaptive capacities of birds appear to have declined, rendering them more vulnerable to external stressors. It is urged that urgent conservation measures, especially of the most threatened species of birds, are necessary.

Keywords: birds; morphology; physiology; flight; adaptation; climate change; pollution

1. Introduction

‘Evolutionary novelty, while often beneficial, frequently comes with associated costs. These costs can manifest as reduced fitness in certain environments, increased susceptibility to specific challenges, or trade-offs with other advantageous traits’. [1]

Recently, it was ardently argued that ‘Darwin’s Theory of Evolution by Natural Selection’ [2], the longstanding overarching biological framework which persuasively explains why, how and when evolutionary changes and adaptive traits develop should from lack of alternative as robust formulations be considered a ‘law’ [3,4]. Multicellular organisms comprise various complex structurally- and functionally reciprocally interdependent parts [5,6]. Synergy between traits fosters outcomes which result in total performance which surpasses the sum of the operations of the individual parts [7–9]. Terms such as ‘integrated phenotype’ [10,11], ‘morphological integration’ [12–14] and ‘symmorphosis’ [15–17] have been used to express the correlations between biological traits, particularly those between structure and function. For animals, from cellular to organ-system levels of organisation, life exists under finite resources of energy, nutrients and time [18–21]. Invariably, allocation of resources to one trait reduces what remains for the others [22,23]. Foremost, genetic-, environmental-, morphological-, physiological- and behavioural factors determine the nature of the biological adaptations which develop to most optimally support life [24–26]. According to Chen and Khanna [27], for the birds of North America, compared to the generalist species, the ongoing climate change is notably impacting the specialist ones. From the ongoing environmental changes (ECs), it is projected that by the end of this century, declines of 7–16% will have occurred for specialist animal species while the generalist ones will have suffered relatively lower losses of 1–3% [27]. While specialist animals operate optimally under specific ECs, their adaptive specialisations may constrain their capacity of adjusting to different ECs [28–30].

To maintain balance while imparting optimization, in biology, adaptive processes entail transactions which comprise trade-offs and compromises [31–33]. The best fitness levels are determined by traits which develop and work together [34–37]. Adaptively well-endowed animals survive and thrive to pass on their ‘good’ genes to new generations [7,34]. Under extreme ECs, such as those existing now, the adaptive capacity of birds appears to have weakened [38–40]. Ancel [41], Price *et al.* [42] and Paenke *et al.* [43] observed that rapid and extreme changes in the ECs constrain adaptability, limiting further specialisations. Adaptations make generalist animals change to specialists and interestingly, depending on the nature and the level of the severity of the ECs, specialist species can change to generalists [44,45]. According to the classical model of biological trade-offs and traits [35], for specialist animals, convex trade-offs support sympatry, i.e., coexistence between species, while concave ones afford development of intermediate ones. Determining how ECs impact ecological diversity instructively informs on the most cost-effective conservation strategies [46–48]. Specialist animals, which are restricted to small ecological ranges and utilise a special kind of food are at greater risk of annihilation from shifts in ECs [49–52]. While specialisation brings about greater extinction risk, exploitation of various resources allows generalist animals to adapt and thrive in adverse habitats [53–55].

In contribution to the ongoing studies, discussions and debates and hopefully stimulate further research on the many indeterminate aspects on the effects of the pressures imposed on the bird life by the present ECs, the following question was posed: did evolution of unique adaptations in birds, ostensibly under different ECs, undermine their capacity of attuning to different conditions such as those existing now? To explain the perspective, the following aspects were considered: a) birds as ‘specialist’ and ‘extreme’ animals; b) the foremost ECs, i.e., climate change and habitat devastation and pollution, which are adversely affecting the bird life and; c) the consequences arising from their living under the challenging surroundings.

2. Birds Are Specialist- and Extreme Animals

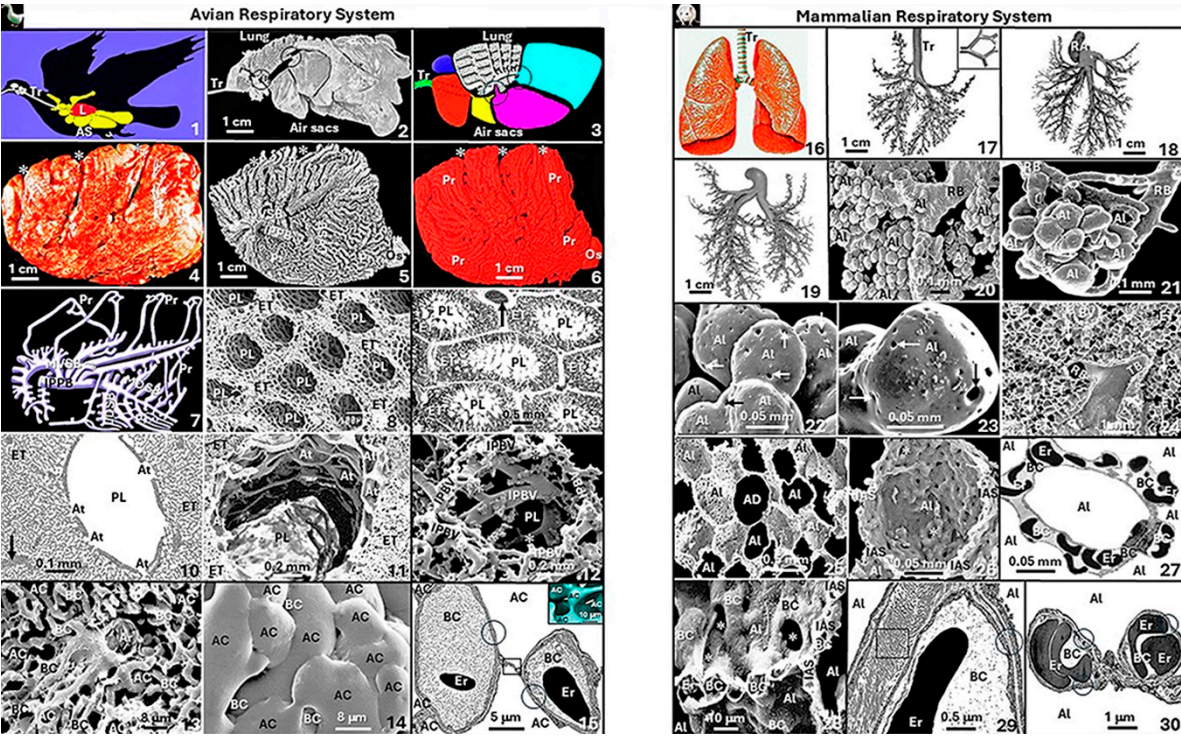
Termed 'living dinosaurs', evolutionary, birds are a unique animal group. They are 'well-oiled machines', which possess diverse adaptive specialisations that have allowed them to globally disperse into various habitats and consequently speciate profusely. Unequivocally, unique biological traits make birds a 'specialist- and extreme' animal taxon [56–62]. During the ~4.3 billion years (10⁹) that life has existed on earth [63–65], only four animal taxa, namely insects, the now extinct pterosaurs, birds and bats, chronologically in that order, have ever accomplished powered flight [66–70]. The adaptive success of birds, which largely afforded their capacity of flight, explains the remarkable speciation into ~11,000 extant species [71–73] which surpass the 3,000 amphibian-, the ~6,000 reptilian- and the 4,100 mammalian ones [74–76]. Volancy, which enabled birds to overcome geographical obstacles such as mountains, rivers, seas, oceans and deserts, permitted them to disperse widely into diverse habitats, causing outstanding adaptive radiation which led to profound speciation [77–79].

Among others, morphological-, physiological-, genetic-, neurological-, reproductive- and behavioral adaptive traits, which suited the habitats they occupied and the lifestyles they pursued, allowed birds to live and thrive, increasing their numerical abundance [58,80–83]. While compared to other modes of travel powered flight is a highly costly type of locomotion, the energetic cost of movement per unit distance covered is considerably less [66,84–89]. For the migratory birds, particularly those which fly continuously for long periods of time over long distances, an activity which occurs under metabolic rates that are ~10 times more than those at rest [90], as much as ~20% of the flight muscle mass is lost due to protein catabolism (breakdown) [91]. The morphological specialisations for powered flight are so restrictive that while the number of species of birds far exceed those of mammals by a factor of about three, regarding their external features, morphometrically, birds are reported to be more uniform than mammals [74,75,92,93]. Even those species that have for various reasons lost flight, i.e., they have acquired secondary flightlessness [94–96], derive from volant progenitors [97,98].

Distinctive biological traits have placed birds high up on the vertebrate evolutionary ranking. The foremost properties include the following: a) the forelimbs were adapted into wings which were fully committed to powered flight [99,100]; b) the skeletal system was considerably modified mainly by loss and fusion of bones and significantly refined for lightness [100–103]; c) the development of large and powerful hearts with strong cardiac muscles generated large cardiac output and short circulatory times which increased O₂- and nutrient delivery to the cells of the body [104–106]; d) loss of teeth [107,108] and their swallowing food whole was countered by development of a food grinding gizzard [109], a feature which contributed to modification of the craniofacial skeleton; e) high and constant body temperatures (38–42°C) permitted elevated metabolic rates [93,106,110–113] which together with powerful flight muscles [114,115] supported active flight; f) an exceptionally efficient respiratory system [58,59,116–118] permitted acquisition of the large amounts of O₂ which sustained high metabolic rates that were vital to powered flight; g) all-encompassing egg-laying (oviporosity) and development of embryos outside of the body, reduced body mass which promoted powered flight [119–122]; h) scrupulous parental care, which included shrewd nest-building and their placement at strategic places ensured survival [123,124]; i) highly developed nervous system with sharp senses allowed important specialised activities such as proper navigation during migration and effective communication [125–127]; j) advanced brains allowed problem-solving capacities, e.g., 'tool use', i.e., dropping hard difficult to break nuts from a height to crack them and access food [128–130] and food caching, i.e., strategic storing of food for use during times of scarcity [131–133]; k) sophisticated vocalisation permitted complex sexual displays and ensured successful mating [134,135]; l) the development of large eyes and excellent visual acuity, especially for the diurnal raptorial species, was important for navigation and effective prey capture [136–138] and; m) light and strong feathers served important needs such as thermal insulation, sexual display, communication and importantly supported flight [139].

Among the air-breathing vertebrates, the avian respiratory system (ARS), the lung-air sac system, is the most structurally complex and functionally efficient gas exchanger

[58,59,75,116,118,140–143]. While its primary function is that of acquisition of O₂ and removal of CO₂, other important roles include sound production at the syrinx [58,75] and thermoregulation [93,144], especially since birds lack sweat glands [144–146]. In biology, research on the form and function of the ARS has been a long and frustrating process which has been riddled passionate debates and controversies [58,116,140–143]. The differences between the structural properties of the ARS [58,147,148] and the mammalian one [149] are respectively shown on Figures 1-15 and 16-30. The incomparable evolutionary-, developmental-, structural- and functional specialisations of the ARS were recently detailed in Maina [58,59]. They include the following aspects: a) the ARS is structurally and functionally divorced into a lung which serves as the gas exchanger and air sacs that work as ventilators (Figures 1-3); b) the lungs, which are small and compact, are firmly affixed to the ribs and the vertebrae, rendering them uninflatable (Figures 1-7); c) structurally, the airway (bronchial) system of the avian lung comprises a three-tier, hoop-like, i.e., continuous, configuration (Figure 7); d) the exchange tissue is intensely partitioned into miniscule terminal respiratory air spaces, the air capillaries (Figures 8-15); e) remarkable morphometric specialisations, which include large respiratory surface area, thin blood-gas barrier (BGB) and large pulmonary capillary blood volume, exist in the avian lung [58,59,147,148] (Figures 14, 15); f) in the exchange tissue, the arrangements of the structural components establish cross-current-, counter-current- and multicapillary serial arterialisation gas exchange systems [58,59] (Figures 8-12); g) synchronized bellows-like actions of the caudal- and the cranial groups of air sacs (Figures 1-3) efficiently ventilate the avian lung continuously and unidirectionally in a caudocranial direction [116,150]; h) for the avian lung, the O₂ extraction efficiency (EO₂) of the ARS, i.e., the ratio of O₂ consumption (VO₂) to O₂ delivery (DO₂) [75] of which the values are as high as 60–70% [150–153] are relatively greater than those of ~20–30% for the nonflying mammals [154,155] and appreciably surpass those of 35–45% for bats (chiroptera) [156,157]; i) compared to the mammalian lung [149], the avian one extracts ~25% more O₂ from the inspired air [106,153] and; j) importantly, from existence of particularly the cross-current- and the multicapillary serial arterialisation gas exchange systems, for the avian lung, the PO₂ in the expired air surpasses those of the arterial- and the mixed venous blood [116,158–161].



AVIAN LUNG: Figure 1 Schematic diagram showing the avian respiratory system (the lung-air sac system). It comprises a lung (L - red) which is separated from and intercalated between the air sacs (AS - yellow). Tr, trachea. **Figure 2.** Lateral view of a latex rubber cast preparation of the lung-

air sac system of the domestic fowl (*Gallus gallus* variant *domesticus*) showing the lung located between the air sacs. Circles (ostia), connections between the air sacs and the lung. Tr, trachea. **Figure 3.** Schematic illustration showing the lung-air sac system of birds. In mature birds, the air sacs comprise cervical- (blue), interclavicular- (red), cranial thoracic- (yellow), caudal thoracic- (pink) and abdominal- (cyan) air sacs. Tr, trachea; circles, ostia. **Figures 4-6.** The compact, i.e., nonlobulated, morphology of the avian lung shown by those of the domestic fowl: 4: Fresh lung (lateral view); 5, 6: Medial- (5) and lateral (6) views of latex rubber macerated cast preparations showing the complex airway arrangement. IPPB, intrapulmonary primary bronchus; MVSB, medioventral secondary bronchi; LVSB, lateroventral secondary bronchi; Pr, parabronchi; Os, ostia; asterisks, costal sulci, i.e., rib impressions. **Figure 7.** Schematic diagram showing the complexity of the airway (bronchial) system of the avian lung. A continuous hoop-like arrangement exists. IPPB, intrapulmonary primary bronchus; MVSB, medioventral secondary bronchi; MDSB, mediiodorsal secondary bronchi; LVSB, lateroventral secondary bronchi; Pr, parabronchi. **Figures 8-11.** Scanning electron micrographs showing parabronchi respectively of the lungs of the house sparrow (*Passer domesticus*) (8), domestic fowl (9, 11) and ostrich (*Struthio camelus*) (10). PL, parabronchial lumen; ET, exchange tissue; arrows, inter- (9) and intra- (10) parabronchial blood vessels; At, atria (10, 11). **Figure 12.** Macerated latex rubber cast preparation of the lung of the domestic fowl showing the parabronchial vasculature. IPBV, interparabronchial blood vessels; PL, parabronchial lumen; asterisks, intraparbbronchial blood vessels. **Figures 13-15.** Exchange tissue of the lung of the domestic fowl shown by a scanning electron micrograph (SEM) (13), a SEM of a latex cast preparation of the air capillaries (AC) and blood capillaries (BC) (14) and a transmission electron micrograph showing same structures (15) at higher magnification. Ar, arteriole (13); circles, blood-gas barrier (15); square, epithelial-epithelial connection (15); Er, erythrocyte (15). Insert - 15: Three-dimensional serial section computer reconstruction showing air capillaries (AC) of the lung of the domestic fowl. **MAMMALIAN LUNG: Figure 16.** Diagrammatic illustration of the lobulated mammalian lung. Tr, trachea. **Figures 17-19:** Latex rubber cast macerated preparations of the pig (*Sus scrofa*) lung showing the airway (bronchial)- (17), the venous- (18) and the arterial (19) systems. The passageways (conduits) branch rather dichotomously. Insert (17), Schematic diagram showing dichotomous branching. Tr, trachea (17); RA, right atrium (18). **Figures 20-23:** Latex rubber cast preparations showing the terminal parts of the airway system of the lung of the baboon (*Papio anubis*) showing pulmonary acini (20, 21); alveoli (20-23); respiratory bronchi (RB) (20, 21) and alveoli (Al) (20-23). Inter-alveolar pore (arrows - 22, 23) and asterisks (23). **Figures 24-28:** Terminal parts of the mammalian (baboon) lung showing alveoli and blood capillaries. Scanning electron micrographs (24-26, 28) and transmission electron micrographs (27, 29, 30). TB, terminal bronchus; RB, respiratory bronchiole; ET, exchange tissue; alveoli (arrows - 24; al - 25-28). BV, blood vessel (24); AD, alveolar duct (25); Al, alveoli (25-28); IAS, interalveolar septum (26, 28); BC, blood capillaries (27, 28); Er, erythrocyte (27); asterisks, interalveolar pores (26, 28). **Figures 29, 30:** Transmission electron micrographs of the baboon lung showing the blood-gas barrier and the interalveolar septa. Circles, blood-gas barrier (29, 30) and square (29), the thicker (supporting) part of the interalveolar septum which contains plentiful collagen fibers (square - 29). Al, alveoli; BC, blood capillaries; Er, erythrocytes.

3. Environmental Conditions, Their Impacts on Birds and Aspects Which Suggest Weakening of Their Adaptive Capacities

3.1. Susceptibility of Birds to Diseases and Injuries by Foreign Particulates

The 'One Health Concept' arose from appreciation that human health is closely associated with the well-being of other animals as well as with the states and conditions of the shared environments and habitats [162–165]. Zoonotic diseases are sicknesses that are naturally transmissible between animals and human beings or vice versa [166,167]. Of the emergent diseases, ~75% of them are zoonotic [168–170]. From the close association between people and animals, especially pet- and companion ones, zoonotic diseases are of important public health concern [171–173]. Migratory

birds, which travel over long distances during their seasonal sojourns, are important transmitters of zoonotic diseases [171,173–177]: they interact with various species of animals and humans during stopovers and at their final destinations [173,177–179]. Rural birds generally visit polluted areas such as sprayed agricultural fields while the urban ones go to contaminated places such as factories, hospitals, dump sites and waste water and refuse treatment plants where they pick up pathogenic microorganisms and toxic chemical substances which they introduce into the food chain by their droppings, carcasses and direct interactions with other animals [180].

While avian migration is a highly rewarding undertaking because birds relocate to sites where food is assured, escape adverse weather conditions and reproductive success is more certain, it is a highly perilous undertaking [181]. The travels entail high energy cost from the strenuous work of flapping flight and exposure to scarcity or lack of food and water and coping with the extreme ECs of the high altitude such as extremely low ambient temperatures, low PO₂ (hypoxia) and dry air [182–184]. During migration, the continuous strenuous work of flight causes muscle damage, dehydration, weight loss, declined immunity and diseases and deaths [91,94,185,186]: immunosuppressed birds are more susceptible to diseases [187–189]. Human incursion into habitats which were exclusively occupied by birds and human pursuits such as taming and domestication of wild birds as pets or for sport as well as the increase of farming, consumption and utilization of poultry products have considerably increased the possibility of pathogenic microorganisms crossing biological (genetic) barriers and triggering zoonotic disease outbreaks [174]. For animals, the immune system (IS) has taken at least 1,000 million years to evolve to its modern status [190]. Evolutionary, the avian IS separated from the mammalian one more than 200 million years ago [191]. While the basic structure and function of the avian IS is similar to the mammalian one, the avian one is structurally less elaborate and more uniform [192,193]. For birds, fewer immunoglobulin classes exist, lymph nodes are lacking and the neutrophils are undifferentiated [194]. The avian IS has certain unique attributes such as presence of the Bursa of Fabricius, a lymphoid organ where B lymphocytes (B-cells) differentiate and mature and a suite of antibodies is produced [194]. According to Cottier [195], developmentally and functionally, the avian IS fits between those of fish, amphibians and reptiles and that of mammals.

The structural- and functional novelties of the ARS have been well-described [58,75,116,140–143,150,152,196,197]. Under ECs that were ostensibly different from the present ones [199], the adaptive specialisations developed in a transactional manner [198]. Birds are particularly susceptible to attacks by pathogenic microorganisms, fungi and parasites and injury by particulate matter, especially those that are acquired by inhalation of air [58,200–203]. The physical- and cellular defenses of the ARS comprise intricate processes which include filtering of air and clearance, isolation, destruction of harmful pathogenic microorganisms and particulates and repair of the injuries caused [204–206]. The notable structural features which make the ARS particularly vulnerable to infections, afflictions and injuries include the following: a) compared with mammals, for animals of equivalent body mass, birds have a respiratory surface area which is 15 % greater, the BGB is 56-67% thinner and the pulmonary capillary blood volume is 22% greater [58,147,148]; b) the protective phagocytic free avian respiratory macrophages (FARMs) are scarce and even lacking on the respiratory surface [58,152,207–211]; c) the exchange tissue is lined by non-ciliated cuboidal- or squamous epithelia which cannot efficiently remove or destroy pathogenic microorganisms and injurious particulates which settle there [152,212]; d) lacking a diaphragmatic partitioning, with some of them pneumatizing bones, the capacious air sacs (ASs) spread extensively in the coelomic cavity [213] and for species such as the ostrich (*Struthio camelus*), some of the ASs exit the coelomic cavity to lie subcutaneously [58,214–217] where they are highly vulnerable to injury especially from trauma; e) from the dispersion of the ASs to most parts of the avian body, diseases and infections affecting the body end up spreading to the ARS; f) the capacious ASs of the ARS provide large tidal volume which leads to delivery of a large measure of pathogens and particulates to the body and; g) because the walls of the ASs are very thin and delicate, poorly vascularized and scantily lined by an epithelium [143,218], the ASs are highly vulnerable to attack and injury by pathogens and particulates and

because of their fragility they provide little protection to the structures of the body which they interface with. Interestingly, evident trade-offs and compromises were involved in the adaptive specialisations of the ARS. For example: a) while lack of FARMs on the respiratory surface promoted respiratory efficiency by decreasing the thickness of the BGB [147,148,219], it made the tissue barrier (BGB) highly susceptible to structural failure and injury by pathogens and particulates [220,221] and; b) while the rigidity of the avian lung allowed intense subdivision of the exchange tissue, a process which generated large respiratory surface, the minuscule terminal respiratory units (the air capillaries) were rendered highly vulnerable to infections and afflictions particularly from scarcity or lack of FARMs from the respiratory surface [219].

Physiologically, the foremost processes which make birds particularly vulnerable to respiratory infections and afflictions are the following: a) during every respiratory cycle, the large tidal volume, which comes from the large ASs, leads to complete turnover of the volume of air in the lung [158], delivering large quantities of pathogens and particulates to the lung; b) from the synchronised actions of the cranial and caudal ASs, the exchange tissue of the avian lung is continuously and unidirectionally ventilated with air in a caudocranial direction, a process which increases the delivery and deposition of pathogens and injurious particulates in the exchange tissue [58,116,150,152,219]; c) for a disease such as aspergillosis [187,222,223], rapid fungal growth has been attributed to the high body temperatures of birds which range from 38 to 42° C and; d) because the inhaled air, which contains large quantities of pathogens and particulates, is shunted to the back of the lung via the intrapulmonary primary bronchus into the caudal ASs [58,59,150,152], compared to the other parts of the ARS, the caudal areas of the avian body are more vulnerable to injuries by inhaled pathogens and particulates [152].

Respiratory diseases are particularly common in the pet- and poultry birds [224–226] where mortalities cause considerable financial losses [202,226,227]. The notable susceptibility of poultry to diseases, especially respiratory ones, may, however, largely derive from the conditions under which the birds are reared [58,228–231]. States and conditions such as overcrowding, poor ventilation, high environmental temperatures and humidities, hypoxia and high concentrations of toxic gases such as ammonia (mainly from putrefaction of fecal waste matter) and possible harsh routine procedures such as poor handling during occasions such as feeding, examination and medication inflict stress on birds particularly poultry [189,231–236]. Stress from adverse ECs weakens the immune system of birds, making them more susceptible to infections and afflictions [231,237–240]. The current high temperatures and those predicted in the future [241,242], especially in the tropics, will worsen the susceptibility of birds to diseases.

3.2. Effects of Climate- and Anthropogenic Habitat Devastation on the Bird Life

The continuing climate- and habitat changes are some of the leading drivers of the losses of biodiversity, population declines and species extinctions [184,241–243]. Among the vertebrates, birds and amphibians are the most vulnerable animal taxa [244–248]. Regarding the impacts of the current changes in the ECs on the animal life, birds are the better studied group [249–251]. The many enthusiastic bird watchers and bird lovers who observe, identify, enumerate and track birds across the world, contribute importantly to the understanding their biology in various ecotopes [252–255]. For their being involved in activities such as eradication of pests and disease vectors, pollination of plants and dispersal of seeds, birds play vital roles of maintaining ecosystem integrities [256–258]. From their global distribution and with some of them migrating over long distances, birds are highly vulnerable to the effects of climate- and habitat changes [245,246,259], conditions which adversely affect their distribution, diversity and numerical abundance [260–264]. With the average global temperature predicted to rise significantly in the future [265,266], extinction rates will increase greatly [267–269]. By the year 2,100, the anticipated 3.5°C increase of the earth's surface temperature will cause extinctions of 600 to 900 species of birds of which 89% of them will be in the tropics [270]. In future, climate change is expected to accelerate at a rate 20 times faster than it has at any time during the last 2 million years [271]. The process will lead to severe ecological range

reductions [272]. Birds with poor capacity of vacating stressful habitats, e.g., the flightless ones, face greater danger of extinction [244]. While certain species of birds are more vulnerable to the effects of climate change than others [255], generally, depending on the nature and the degree of susceptibility, species of birds which possess extreme attributes such as small body size are, compared to the larger ones, at greater risk of population decline and extinction from changes in ECs [273–275]. While for the evolutionary ‘older’, i.e., ‘ancestral’ or ‘basal’, species phylogeny affects the social organisation of bird populations by increasing the size and the range of their habitats, for the ‘recent’, i.e., derived species, phylogeny determines species abundance [276,277]. Because extreme ECs decimate occasional species, it is expected that in future birds will become more homogenous in aspects such as body size and shape [276–278].

Regarding the onsets of their travels and breeding times, for the migratory species of birds, climate change has particularly considerably impacted on the timing of their seasonal travels [246,279–281]. With catastrophic consequences, loss of stopover habitats has made birds fail reaching their breeding sites on time or not at all [241,244,282–284]. Late starting- and arrival times are a common cause of the declines of the migratory bird populations [279,281,285–287]. Disordered food webs, changed breeding seasons, reduced survival and reproduction rates, increased disease incidents, changes in ecological ranges and population declines are indicators of the adverse effects which changed ECs are having on the animal life [244,246,288–290]. Haile [291] and Radchuk *et al.* [292] observed that presently, birds are exhibiting signs of incapacity of adjusting to the pressures they are facing from the prevailing ECs. Alternatively, the birds may not be responding fast- or adequately enough to the challenges presented by the ECs. Interestingly, for the caribou or the reindeer (*Rangifer tarandus*), Canteri *et al.* [293] reported that while the species well-tolerated a sudden climatic warming event during the last deglaciation episode (~21,000 years ago), the animals are now experiencing marked worldwide numerical decline. While the investigators did not give a specific reason for the decrease in numbers, it is plausible that they may now have lost their adaptive capacity to the present extreme ECs. For birds, the adaptive novelties which may have served them well in the past under different ECs may now have rendered them unresponsive under the prevailing extreme conditions.

Significant population recoveries of threatened species can conceivably be reversed by adopting species-focused, broad-based conservation strategies which include aspects such as habitat restoration, captive breeding and release and community awareness and involvement [294–296]. Interestingly, recently, Cullen *et al.* [297] reported that the once nationally endangered Australian amputa (*Dasyercus hillieri*), a rat-sized marsupial micro-predator, has defied all odds and the numbers have significantly recovered: the population rebound was attributed to aspects such as a remarkable increase of ecological range, flexible diet and physiological adaptation to low energy food. It shows that compared to specialist animal species, generalists may stand a better chance of successfully adjusting to environmental perturbations. While external morphological features such as the sizes of the tail, wing, mid toe, tarsus, beak width, beak length and beak depth, which have been argued to correlate with the ecological differences between avian taxa [298–300], have been used to determine how specialisations may have driven diversification at different levels of population organisations, interpretations and views have varied between investigators. Foremost, this may be because the external morphologies of birds are unlikely to utterly represent the correlations between the avian morphologies and their diverse ecological choices.

3.3. Effects of Environmental Pollution on Birds

The increasing global level of environmental pollution is critically impacting on the survival of the animals life especially that of birds [246,301,302]. By causing among others suppression of the immune system, birds are becoming more vulnerable to diseases, injuries and poisoning [246,302–305]. From their high metabolic rates [110–113,306], particularly for the migratory species of birds which perform strenuous sustained flights over long distances [307,308], production of large quantities of reactive O₂ species causes oxidative tissue injuries [309–311]. Also, the high metabolic

rates of birds increase production of toxins [312,313]. From their numerical abundance and global distribution, at various places, birds are exposed to different ECs and consequently to varied pathogenic microorganisms and contaminants [173,314–316].

Birds are well-known 'biosensors', 'bioindicators' or 'sentinels' of environmental pollution [314,315,317–321]. Their sensitivity to changes in the ECs makes them important early warning animals of ecosystem hazards [318]. Smith *et al.* [322] determined that for birds, air quality correlates with species diversity, numerical abundance and breeding success while Fry [323], Abbasi *et al.* [324], Sanderfoot and Holloway [314], Shore and Taggart [325], Maznikova *et al.* [326], Castagna *et al.* [327] and Vetere *et al.* [328] noted that in accord with other apex predators, birds are highly susceptible to toxins and pollutants which they largely acquire from the air they breathe, foods they eat, water they drink and from physical contact with their surroundings. Depending on the nature and level of pollution in a habitat and the state of immune suppression, which usually occurs under various stressful conditions, birds are particularly susceptible to diseases and injuries [234,314,316,329]. Birds exposed to PM_{2.5} size particulates have high macrophage infiltration and small lung volumes [330]. Feral pigeons exposed to inhalation of nitrogen oxides (Nox) have lower erythrocyte counts and high oxidative stress markers [331]. Liang *et al.* [332] reported that the decrease of the numbers of migratory warblers across North America was attributable to ozone pollution. Jat *et al.* [333] observed that air pollution seriously affects the migratory behaviours of birds. Increased exposure to PM_{2.5} size particulates at a concentration of 120 µg/m³ caused the bar-headed geese (*Anser indicus*) and the Arctic terns (*Sterna paradisaea*) to stray from their normal migratory paths across the Indo-Gangetic Plain by a distance of as much as 250–320 km.

Because of the high energetic cost of flight, which is aggravated by the effect of pollution, Hedenström and Hedh [334] noted that long-distance migratory birds suffer severe metabolic stress and have relatively shorter longevity. In the coal mining parts of China and India, high mortality rates of birds, low species diversity and respiratory distresses were reported [335]. After the birds were exposed to smoke from wildfire, for a time afterwards, song complexity and performance were reduced by a factor of 15% [336]. Sanderfoot and Holloway [314] observed that together with deteriorating lung function, birds exposed to highly toxic gases and injurious particulates presented histopathological injuries of the respiratory tissues. In various ways, compared with the mammalian respiratory system (Figures 16-30), certain aspects of the morphological- and physiological specialisations of the ARS (Figures 1-15) [58,116,143,147,148,219] predispose birds to attack by pathogenic microorganisms and injury by particulates.

4. Conclusions

The evolutionary progress of birds is well-reflected in aspects such as their global dispersion, their remarkable speciosity, numerical abundance and the diverse lifestyles they pursue. Presently, the marked reduction of the avian biodiversity and the increase in the rates of extinction are largely driven by ongoing harsh ECs which include global warming, pollution and habitat devastation. Some of the results inflicted by the ECs on birds include high susceptibility to diseases (especially pulmonary acquired ones) and inability to adequately respond to physiological challenges such as suffering heat burden. Cage birds are particularly vulnerable to conditions like hyperthermia which may arise from poor physiological thermoregulatory capacity [232,337,338]. Extreme environmental temperatures negatively affect bird health [339–341]. This is particularly worrisome because modeling studies have predicted that temperature will continue to rise for the rest of this (21st) century [342–344]. The migratory birds will particularly face multiple challenges such as devastation of their stop-over sites, deaths from extreme weather conditions and food and water scarcity. Presently, seabirds are among the most threatened group of birds [345,346].

The notable decrease in avian biodiversity may especially be explained by the fact that while the development of adaptive traits is a drawn-out process, the severity of the ECs may be increasing at a rate faster than that by which the birds are attuning to the changes. Given the existential threat, conservation of birds, especially the threatened and endangered species, is urgently warranted. The

resilient nature of the animal life in general and that of birds in particular to threats presented by the ECs is astounding. For example, between the years 1970 and 2022, the estimated spring population of the lesser snow geese (*Anser caerulescens caerulescens*) in the Pacific Flyway of North America increased from ~300,000 to ~2,300,000 [347]. The increase was attributed mainly to changes in productivity in the Western Arctic and productivity and immigration in Wrangel Island. Knowing the most important measurable biological- and ecosystem parameters which signal early presence of environmental stressors should allow timely intervention and possibly reversal of damages [346]. In attempt to contend with different ECs, some bird species have acquired distinctive adaptive plasticity which has lead to unique foraging abilities and nesting behaviours [347–349]. For meaningful prediction of how birds in particular respond to extreme conditions, different spatial- and temporal factors which impact on their health should be considered [350,351]. Regrettably, for now, data on the biological- and ecological ‘tipping points’ of many species of birds are lacking [351]. Such details can be importantly leveraged to enhance conservation efforts.

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