Ecophysiology of avian migration in the face of current global hazards

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Long-distance migratory birds are often considered extreme athletes, possessing a range of traits that approach the physiological limits of vertebrate design. In addition, their movements must be carefully timed to ensure that they obtain resources of sufficient quantity and quality to satisfy their high-energy needs. Migratory birds may therefore be particularly vulnerable to global change processes that are projected to alter the quality and quantity of resource availability. Because long-distance flight requires high and sustained aerobic capacity, even minor decreases in vitality can have large negative consequences for migrants. In the light of this, we assess how current global change processes may affect the ability of birds to meet the physiological demands of migration, and suggest areas where avian physiologists may help to identify potential hazards. Predicting the consequences of global change scenarios on migrant species requires (i) reconciliation of empirical and theoretical studies of avian flight physiology; (ii) an understanding of the effects of food quality, toxicants and disease on migrant performance; and (iii) mechanistic models that integrate abiotic and biotic factors to predict migratory behaviour. Critically, a multi-dimensional concept of vitality would greatly facilitate evaluation of the impact of various global change processes on the population dynamics of migratory birds.

Keywords: migratory; habitat destruction; climate change; conservation; avian physiology; vitality

1. INTRODUCTION

Migratory birds face extreme physiological challenges. Recent studies have revealed some astounding feats among migrants, such as the week-long, non-stop flights of bar-tailed godwits (Limosa lapponica) crossing the Pacific between the Arctic and New Zealand, a distance of over 10 000 km [1]. These long-distance flights entail intense metabolic and navigational demands [2], often in hostile high-altitude environments, at low ambient temperatures, low partial oxygen pressures and low humidities [3]. Prior to migration, and at intermittent stopover sites en route, migratory birds undergo major physiological adjustments to enable rapid accumulation of fuel stores, which can result in up to a threefold increase in body mass [4]. They must then undergo rapid physiological and morphological adjustments that transform them from organisms that maximize their gains from foraging to organisms that maximize their potential flight distance, making them exemplars of phenotypic plasticity [5]. Along the various migratory flyways that span the globe, approximately one-fifth of all extant bird species migrate long distances, in search of benign weather, improved safety, increased foraging opportunities and higher reproductive output. Despite the challenges of these long-distance movements, scientists have been unable to identify a migratory syndrome that is common to migrating species, suggesting that there is no typical suite of adaptive traits that truly distinguishes migratory birds from non-migrants [6]. Nevertheless, it is widely acknowledged that migratory birds may easily approach physiological limits with respect to a wide range of traits. Apart from the alternating behaviours of maximum fuel-loading before flight and distance-maximizing while flying, other parts of their life cycle are equally important for maintaining populations. Migrants must both avoid risks to survival (e.g. predation, diseases, exhaustion) and maximize access to resources that improve success in other important processes during the annual cycle (such as moult and reproduction). Given the high physiological demands of migration and their reliance on widely dispersed stopover habitats along their extensive flyways, migratory species would appear to be particularly vulnerable to global change processes.

Climate change, together with other global change processes such as land use changes, habitat destruction and fragmentation, is increasingly considered to endanger migratory birds by increasing distances between suitable stopover sites and causing mismatches in timing of departure in relation to occurrence of peak food availability at distant locations. These impacts on
migrants may also have ecological ramifications at community and ecosystem scales, because migratory birds provide many ecosystem functions and services, such as pest control, assistance in dispersal of other organisms, pollination and nutrient cycling [7–9]. There is also increasing interest in how migratory birds may affect the abundance and distribution of diseases that threaten humans, such as highly pathogenic avian influenza virus H5N1 originating in Southeast Asia, and West Nile virus in the Americas [10]. Consequently, studies addressing the potential for migratory birds to assist in the spread of these pathogens, and how global change processes will affect this, are gaining urgency.

In view of current global changes, it is opportune to consider how increased rates of environmental alteration might affect migratory species. These changes need not be negative per se; there are examples of anthropogenically altered environmental conditions benefiting particular migratory species, such as many herbivorous waterfowl that profit from agricultural intensification [11]. Nevertheless, emerging evidence shows that populations of long-distance migratory birds are declining more rapidly than those of resident bird species, both in North America and in Europe [12,13], reaffirming the notion that long-distance migrants may be very susceptible to global change processes.

We examine three main physiological attributes that we identify as being of prime importance to the fitness of migrants: vitality (as the overall requirement to avoid death and maximize success, be that of migration or any other stage during the annual cycle), body stores (as prime determinant of flight range and ability to meet nutritional needs) and fuelling rate (as a prime determinant of speed of migration). These attributes interact in permitting a bird to move the required distance in the appropriate timeframe. We have intentionally avoided using body condition as derived from body stores as a proxy for animal ‘health’ for two reasons. Firstly, condition indices based on extent of body stores presume that animals with greater mass relative to their size have more body stores and are thus healthier than those with relatively less mass [14]. While very low body condition by such measures can be associated with under-nutrition and consequent poor health, the converse is not necessarily true. In fact, animals maintaining body stores in excess of energy and nutritional requirements for a given life stage are likely to be more vulnerable to predators owing to the increased daily feeding requirements to maintain excess mass, but also because of reduced escape speed and manoeuvrability when attacked [15]. Thus, body condition would be expected to vary dynamically in accordance with the balance between energy storage needs and predation risk [16]. Our second reason for not using body condition indices as a proxy for animal health is that body stores influence vital function not simply by their amount, but also by the quality of their contents [17]. This is especially true not only for essential fatty acids, but also for critical amino acids during times of reduced feeding or fasting. We thus feel that health is better inferred from a combination of vitality and body store measurements made with reference to seasonally relevant baselines.

In the following review, we present evidence to suggest that global change perturbations, with its concomitant changes in a wide range of biotic and physical factors, are likely to adversely affect the three core physiological attributes (vitality, body stores and fuelling rate; figure 1). These factors may result in reductions in habitat size (including the loss of stopover sites, decreased food densities and increased competitor densities), reductions in habitat quality (including exposure to disease, toxicants, reductions in food quality and increases in disturbance and predation), or climate-induced changes to phenology and physical conditions while en route (including the direct impact of severe weather events and increasing ‘time stress’ faced by migrants). Each of these is discussed in terms of their influence on the three core physiological attributes. In doing so, we identify the lack of physiological understanding for many of the mechanisms governing these interactions, and suggest directions for future research. To facilitate referral to figure 1, we have italicized the various global-change-related effectors and emphasized the affected core physiological attributes in bold type throughout the text.

2. REDUCTIONS IN HABITAT SIZE
The quest for food during the energy-demanding migratory period often funnels migrants into the most productive areas globally, areas also favoured for human habitation and agricultural production. Forty per cent of the Earth’s land mass has now been cultivated. Worst still, this is some of the most productive land, nature reserves mainly being established in what would otherwise have been wasteland to man. This realization identifies considerable potential for conflicts between man and migrants. Indeed, for the global decline of migrant’s habitat, destruction has been considered as one of the main causes [18]. Below, we address how habitat reduction and destruction may constrain and ultimately endanger migrants.

(a) Food density and competitor density
Migrating species devote most of the migration period to foraging in order to fuel their flight [19,20]. Consequently, the speed at which birds migrate is largely determined by the rate at which they can forage and replenish their stores, i.e. their fuelling rate. Clearly, the rate of fuelling is dependent on the availability of food, and hence the availability of foraging habitats. Habitat destruction may lead to either the complete loss of stopover sites, or reductions in food density, both directly and indirectly through an increase in competitor density, which has been shown to negatively affect fuelling rates [21,22]. Furthermore, competition for food may affect vitality both from reduced access to nutrients as well as increased levels of stress, both of which may lead to reduced immunity and poorer health.

During the migratory period, some birds are capable of ingesting vast quantities of food, provided they can forage without disturbance for 24 h day−1 in high-quality environments [20]. In situations of high food density (and low competitor density), the phenotypic adjustments of long-distance migrants may push their
maximum intake rate to exceptional levels \[5,23,24\]. These intake rates, however, depend on species size, with the rate of migration being inversely related to body size owing to size-related physiological constraints on rate of energy assimilation \[25\]. As a consequence, large birds may be particularly disadvantaged by habitat size reductions and accompanying decreases in food density, or increases in competitor density. (b) Loss of stopover sites

Large birds may also be more vulnerable to the total loss of stopover sites. As flight distances increase, more fuel in the form of body stores is required to fuel the journey, resulting in higher body mass. Indeed, according to aerodynamic theory, increases in mass impose increasingly higher flight costs and will ultimately limit a bird's flight range \[26\]. Aerodynamic theory also predicts maximum flight range to decrease with increasing body size \[26\]. Empirical findings are somewhat out of line with aerodynamic theory. The additional flight costs concomitant to carrying this extra mass are lower than predicted \[27,28\], while empirical evidence shows flight range to actually increase with increasing size up to approximately 2 kg; however, maximum flight range tends to decrease thereafter \[29\], highlighting the potential for habitat loss to disproportionately impact on larger species. Moreover, as pointed out below, time stress may necessitate larger birds in seasonal environments to arrive on their breeding grounds with extra body stores. In larger birds, body stores are thus required to guarantee not only an adequate flight range but also successful breeding.

3. REDUCTIONS IN HABITAT QUALITY
(a) Disease

Although parasitism and disease are impacting on the vitality of all organisms, their association with migrants differs from that of non-migrants for three reasons: (i) migrants are potentially important vectors for the long-distance dispersal of parasites; (ii) their travels may expose them to more pathogens than encountered by resident species; and (iii) the physiological demands of long-distance migration may lead to a dampening of their defence responses, and thus a higher susceptibility to disease. Moreover, emerging infectious diseases in the human population have increased significantly over the past century, with many of these diseases originating from wildlife \[30\]. As a result, there is increased interest in how anthropogenic degradation of the environment may not only make migrants more vulnerable to disease but also increase the spread of pathogens with immediate relevance to man \[10\]. Although migrating animals may potentially disperse pathogens over long distances and disparate habitats \[31\], surprisingly few examples have been documented \[10\]. For instance, there is considerable
debate on the importance of migratory birds in the spread of the H5N1 highly pathogenic subtype of avian influenza virus, a pathogen of significant concern for both public health and domestic poultry production [32,33]. Importantly, migratory waterbirds (waterfowl Anseriformes and waders/gulls Charadriiformes) are considered an important reservoir for low-pathogenic avian influenza viruses, certain strains of which represent precursors for highly pathogenic avian influenza viruses [34,35]. Although avian influenza is currently in the spotlight, there are numerous other diseases for which migratory birds may be important vectors [36].

In principal, migration may increase an individual’s exposure to pathogens as a result of the number of sites and habitats used while en route. Studies on blood parasite loads have shown that migrants may indeed be at higher risk of infection from a more diverse range of parasites, both on the basis of migratory distance [37] and in comparison with resident birds [38]. In addition, animals tend to aggregate during periods of migration, often making use of hotspots of food abundance to rapidly restore body stores en route, which can further increase their disease infection risk [39,40, but see 41]. Continuing human encroachment on these migratory stopover sites increases both the likelihood of contact and spill-over of infections from wildlife reservoirs to humans and domesticated species [10], and the other way around (i.e. the spill-over of diseases from humans and domesticated animals to wildlife) [42,43]. Conversely, migration may act to reduce infection risk. Empirical studies indicate that the prevalence of particular pathogens or parasite species may be comparatively lower in migratory populations [44,45]. Two complementary explanations for this pattern are that (i) migration allows animals to periodically escape locally contaminated habitats (‘migratory escape’); and (ii) long-distance migration weeds out infected animals (‘migratory culling’) [10,39]. As a result, reduction in or loss of migratory behaviour may result in an increase in disease risk [10].

In order to minimize the impact of infectious diseases on their vitality, animals have developed a complex arsenal of defence strategies to both tolerate and resist pathogens [46]. Perhaps foremost among these is a multifaceted immune system (for a concise description, see Buehler et al. [47]). The activation and maintenance of these defence strategies imposes significant nutritional and energetic costs on the host, and, as a result, investments in defence against infection are likely to trade-off with other physiological processes, including fuelling rate [48]. These trade-offs may be particularly acute in migrants, given the costs associated with long-distance flight [47]. Indeed, exercise physiologists have extensively demonstrated that comparable levels of physical exertion in humans are associated with a dampening of their immune responses [49]. Therefore, as a result of exercise-induced dampening of the immune system, actively migrating birds may be more susceptible to infections, or more likely to experience a reactivation of latent infections than during less-demanding phases in the annual cycle [10,50]. Any additional stresses resulting from environmental perturbations may further heighten this susceptibility [49].

Given the potential for migrants to encounter a greater diversity of pathogens (as outlined above), dampening of the immune response seems an unwelcome complication; humans preparing for similar journeys regularly acquire vaccinations to pathogens prevailing at their destination. On the other hand, dampening of the immune system may, aside from potentially permitting the reallocation of resources from immune functions to physical activity and flight machinery, better ensure high refuelling rates at stopover sites. This is because activation of certain immune responses, particularly initiation of acute phase responses, can result in a significant reduction in appetite and lethargy [51]. For migrants, who refuel at levels approaching maximal intake rates [20], an immune-induced reduction in appetite could adversely affect their chances of successful migration and breeding. Furthermore, dampening immune reactions may also reduce the risk of autoimmune responses [52], particularly against the increased cellular damage resulting from extended periods of physical exertion. In the face of these additional considerations, actively migrating animals might thus benefit from a greater tolerance to pathogens rather than resisting them. However, it is questionable if, in the face of various global change processes, the cost–benefit trade-off in immune function remains unaffected and natural levels of immune function are sufficiently adequate.

Pathogenic infections have the potential to affect the vitality and migratory ability of animals. For instance, an outbreak of H5N1 highly pathogenic avian influenza virus in bar-headed geese (Anser indicus) bred at Qinghai Lake in China in 2005 culled 10 per cent of the global population [53]. Although a potentially extreme example, such cases highlight the imperative to better understand the role of migration in modulating disease dynamics, particularly factors influencing individual susceptibility to infection, behavioural alterations as a result of infection and how such changes in behaviour will influence transmission. There is some evidence that susceptibility to infection may differ between individuals on the basis of age and infection history [54], and throughout the annual cycle. There is, however, no comprehensive understanding of the mechanisms constraining resistance and tolerance to infection among individuals. Similarly, our understanding of the impact of infection on movement behaviour is relatively limited. In migratory monarch butterflies, protozoan infections have been shown to reduce flight speed and endurance [55]. Similarly, although the majority of ducks infected with low-pathogenic avian influenza viruses under laboratory conditions show no clinical signs of infection, naturally infected Bewick’s swans (Cygnus columbianus bewickii) under field conditions, where birds have to acquire food, avoid predation and thermoregulate, show significant reductions in their pre-migratory fuelling rate and movement behaviours [56]. Importantly, delays in movement of infected individuals of the magnitude reported [56] have the potential to alter the timing and intensity of yearly epidemics of avian influenza virus in wild birds [57]. Increased insight into the mechanisms underlying both susceptibility to infection and the impact of infection on host behaviour are clearly needed to understand.
the dynamics of infectious diseases [58], and interpret potential perturbations in the face of global change.

(b) Toxicants

The release of a wide range of toxicants through anthropogenic activities has a major impact on ecosystems globally [59]. Increased use of agrochemicals and petroleum products worldwide [60], as well as the increased reliance of wild animals on anthropogenic habitats may impose distinct risks to the vitality of migratory animals, as a direct result of their behavioural and physiological traits. For instance, in order to fuel for migratory flight(s), migrants typically engage in gorging feeding, whereby their food intake rates greatly exceed their daily energy needs. Maximizing fuelling rate alone will expose them to higher amounts of toxicants in the local environment, as shown by seasonal changes in food intake and corresponding cycles of fattening and emaciation in Arctic animals [61]. Choice of foraging site may further exacerbate toxicant uptake during hyperphagia, as migratory animals tend to use sites containing dense aggregations of food for migratory preparation and refuelling and these sites are frequently the targets of agricultural pest control. Moreover, lipid-soluble toxicants are likely to accumulate in body stores, such that during endurance flight(s) the amount of toxicants being released as fat is metabolized will be far higher than a resident will experience while foraging in the same contaminated habitat. Although no studies have been conducted in migrants to date, evidence in support of this notion can be gleaned from the increased circulating levels of fat-soluble polychlorinated biphenyls (PCB) concentrations seen in northern elephant seal pups (Mirounga angustirostris) when they mobilize lipids from their own body reserves during their post-weaning fast [62]. Importantly, lipid-soluble organic pollutants are generally recognized for having greater potential for biomagnification in the food chain than water-soluble ones, and for being released from stored fats in birds and mammals when these reserves are mobilized for energy-demanding activities [63]. Critically, any such increase in circulating toxicants through the mobilization of body stores in migratory birds will coincide with periods requiring both peak aerobic performance (or peak metabolic rate, PMR) and endurance. Finally, even low levels of a number of toxicants have been shown to interfere with memory and learning in humans [64], which suggests that these toxicants may have particular relevance for migratory birds that rely heavily on neurosensory mechanisms to navigate between the various sites along their route.

From the above, there is a high potential for toxicants to affect migrants. Although numerous studies have demonstrated correlations between exposure to toxicants and reduced body stores as well as some vitality indices [65], reduced reproductive success [66–68] and even large-scale mortality events in migrating Swainson’s hawks [69], mechanistic links between toxicant exposure and reduced performance of migratory birds are currently lacking. Evidence from non-migrants suggests that toxicants may alter a broad range of physiological processes, often in the absence of clinical signs but nevertheless with adverse effects on fitness. For instance, experimental exposure to the organophosphate pesticide fenitrothion reduced PMR during flight by 18–58% (depending on dose and species) in house sparrows (Passer domesticus), zebra finches (Taeniopygia guttata) and king quails (Coturnix chinensis), and these birds took up to 21 days to recover their PMR [70]. Similarly, fenitrothion reduced running endurance of fat-tailed dunnarts (Sminthopsis crassicaudata, a dasyurid marsupial) to less than half the endurance of control dunnarts for more than a week after dosing. This latter study, however, showed no impact on PMR, suggesting fenitrothion-induced exercise fatigue was not due to limitations in oxygen or substrate delivery to muscle or in their uptake per se, but more likely related to decreased ability to sustain high-frequency neuromuscular function [71]. Such aerobic and locomotor impairments may be of profound importance to migratory species. Other studies have suggested that exposure to toxicants has the potential to alter a bird’s flight capabilities owing to the impact of the toxicant(s) on feather growth. Tail feathers grew at decreased rates, and reached shorter total lengths in great tits (Parus major) following experimental exposure to lead [72]; primary feather asymmetry increased with increasing concentrations of circulating PCB congeners (oxychlorodane, dichlorodiphenylchloroethylene and hexachlorobenzene) in glaucous gulls (Larus hyperboreus) [73]; and flight feathers grown in the presence of high circulating corticosterone (which has been associated with higher heavy metal concentrations in the blood) [74] were lighter, potentially weaker, and showed altered feather micro-structure [75]. Finally, a number of impacts of toxicants on neurobehavioural functions have been described, primarily in humans and in laboratory animal models, with a clear increase in susceptibility in developing embryos and children [64,76]. These differences in susceptibility are a result of the developing brain lacking a blood–brain barrier, which in adults prevents the passage of many endogenous and exogenous toxic agents into the brain [76]. Such neurological difference may explain the dramatic reduction in hatchability and development of zebra finch chicks following experimental exposure of mothers to sub-lethal levels of the new-generation pesticide fipronil, which is increasingly favoured over traditional pesticides because of its greater efficacy on invertebrates [77]. These effects were apparent even at doses that resulted in asymptomatic responses in adults. As these studies in non-migrants demonstrate, many processes key to the success of migrants may be altered by exposure to toxicants, but much work is needed to verify hypotheses and assess these impacts in migrants directly.

(c) Food quality

Body stores of migrating birds consist primarily of fats and protein (and associated water) [78]. In order to fuel their movements, migrating birds rely mainly on stored fat. Because ingestion of food of any type in excess of a bird’s daily requirements can be used to synthesize fat, it would seem that migrating birds need only to increase their daily intake rates of any...
digestible food type to accrue adequate energy stores for long-distance flight. What this ignores, however, is that vertebrates are limited to synthesizing only saturated (SFA) and monounsaturated fatty acids (MUFA) from non-lipid sources and therefore require dietary intake of polyunsaturated fatty acids (PUFA) to provide critical constituents of their species-specific membrane phospholipids [79]. There are two physiologically important types of PUFA which differ in the location of the first double bond on their fatty acid chain; these are the omega-3 (n-3) and omega-6 (n-6) PUFA. Animals differ considerably in their membrane requirements for n-3 and n-6 PUFA [80], but, importantly, vertebrates and most other animals lack the ability to interconvert these and each type of PUFA must, therefore, be gained from food sources. Both types of PUFA are predominantly of plant origin, with n-3 being dominant in chloroplast membranes (thus in leaves), whereas n-6 is the major PUFA of seeds. As a consequence, animals having aquatic plants and phytoplankton as major components in their food chain are biased towards n-3 PUFA, whereas granivores will have an n-6 PUFA bias in their food sources [79].

Because the fatty acid composition of membrane phospholipids affects both membrane-bound enzymatic processes [81] as well as rates of intestinal absorption, transport and uptake by muscles [17,82,83], there is increasing interest in the influence of dietary PUFA on flight endurance and vitality in general. It has been recently suggested that the increased dietary intake of n-3 PUFA-rich vertebrates by semipalmated sandpipers (Calidris pusilla) preparing for migration resulted in improved aerobic capacity by improving rates of oxidative enzymes, mainly via changes in membrane PUFA composition [84], an outcome they termed ‘natural doping’. Because increased aerobic capacity often follows from increased exercise, the extent to which the sandpiper’s diet actually contributed to aerobic improvement was equivocal. Nagahuedi et al. [85] then showed general increases in oxidative enzyme activities in sedentary bobwhite quail (Colinus virginianus) given n-3-enriched diets compared with those getting n-6 enrichment, but the results were not entirely consistent. Furthermore, increases in oxidative enzyme activities do not necessarily lead to improved aerobic performance. A comparison of PMR in flying house sparrows showed that pectoral muscle mass better accounted for differences between individuals than differences in citrate synthase content or total activity [86]. Other studies have found that n-6 PUFA diets engendered improved PMR in flying white-throated sparrows (Zonotrichia albicollis), but through their presumed effects on rates of uptake by muscles rather than through membrane phospholipids [87]. Conversely, incorporation of higher levels of dietary n-3 PUFA in rat (Rattus norvegicus) muscle membranes imparted greater fatigue resistance and improved contractile recovery, with in vivo hindlimb muscle preparations consuming less oxygen for a given workload than those from rats fed either n-6 PUFA- or SFA-biased diets [88]. Given the mixed effects that types of PUFA have in rates of fat transport and uptake by muscles as well as in membrane-dependent enzymatic functions, it would be very worthwhile to examine the consequences of n-3 versus n-6 biased diets on distance between refuelling sites and speed of migration in long-distance migrating species. There is opportunity to examine this through natural experiments by comparing migratory outcomes in populations of shorebirds feeding mainly on seeds at staging areas versus those feeding on aquatic invertebrates (M. Klaassen 2005, personal observation).

Protein also forms an integral part of the tissue synthesized during fuelling and catabolized during migratory flight [78], and dietary proteins are therefore the other important food quality concern for migrating species. It has been suggested that protein loss during flight may be explained by a variety of factors, including (i) adaptive changes in the size of flight muscles and digestive organs in order to minimize energy costs and to increase flight range; (ii) the requirement for gluconeogenesis and anaplerosis of Kreb’s cycle intermediates; (iii) endogenous protein turnover; and (iv) a source of water during long-distance flight particularly under dehydrating conditions [89]. Prior to migration, a suite of hormonal and behavioural changes occurs that promotes rapid gains in body lipids and hypertrophy of flight musculature. The substantial accrual of highly aerobic tissues and their associated enzymes requires provision of the full complement of essential amino acids and, thus, the quality of dietary proteins is important. Similarly, successful migration relies on well-functioning feathers that have the strength and resilience to withstand the mechanical stresses associated with flapping flight to maintain optimal aerodynamic performance [90]. Because feathers are over 90 per cent protein, mainly keratins, and comprise about 10 per cent of a bird’s total mass, they represent about 25 per cent of its total protein content [91]. Furthermore, feathers rely particularly on sulphur-rich amino acids such as cysteine for their synthesis, making protein quality particularly important during this phase of a migratory species’ life cycle [91]. For so-called ‘capital breeders’, which rely on the deposition of extra stores to allow for immediate onset of breeding upon arrival on the breeding grounds, protein accretion may be particularly important for egg synthesis in females. Although it has been suggested that intensively managed grasslands fail to provide geese with the necessary nutrients for an adequate deposition of protein they would otherwise gain from their traditional natural grassland feeding habitat [92], this could not be substantiated by recent in-depth research [93]. Nevertheless, food quality remains an important determinant of a migrant’s vitality and deserves considerable attention when evaluating the impact of global change processes on migrants.

(d) Disturbance and predation

Predation or hunting may have considerable direct mortality effects on migratory birds. Each year, for instance, an estimated 500 million migratory birds are killed in the Mediterranean region alone (http://www.birdlife.org/action/change/sustainable_hunting), almost a quarter of all birds passing [94]. But besides direct mortality, there may be also more subtle fitness effects. As mentioned earlier, their reliance on readily available food resources to fuel their energy-craving migrations often
guides migrants to productive areas globally where human population densities also tend to be high. Ever-increasing levels of disturbance and predation risk have been shown to importantly change the behaviour of migrants, potentially leading to reductions in fueling rates [95,96]. On the basis of a large body of literature on the impacts of chronic stress on man and many animal models, it is very likely that increased chronic stress levels also have impact on the vitality of migrants, but direct data on the impacts of increased disturbance on the health status of migrants are thus far lacking.

4. RESOURCE PHENOLOGY AND WEATHER CONDITIONS

(a) Weather conditions
Various studies have indicated that migratory birds depend on favourable wind patterns to extend their flight range with a given amount of body stores [97–103]. Some bird species, in fact, are believed to be unable to complete their migratory journey without substantial wind assistance [104]. Wind conditions are stochastic, and some species have been found to use intermediate stopover sites for emergency refuelling when confronting unexpected headwinds [105]. Although we lack predictions of how wind patterns may change in response to global change processes, such factors must be taken into account when considering global change consequences on flight range. One of the climate change predictions is an increase in extreme weather conditions, which may additionally challenge migratory birds. Significant mass-mortality events among migrants as a result of extreme weather conditions are well documented, both during migration and at the breeding grounds. These have led to local population size reductions by as much as 90 per cent, occasionally involving millions of birds in single events, and with migrants generally appearing to be much less resistant to inclement weather than resident species [106].

(b) Time stress
Climate change poses three major challenges for migratory birds: (i) changes in climate are not identical or even correlated across the globe; (ii) not all organisms, communities and ecosystems respond in synchrony to such changes; and (iii) ecosystems are not uniformly distributed. These interacting factors may lead to habitat size and habitat quality reductions, adding on to other global change effects whose impacts on the migrants’ physiology were discussed above. Yet, these interacting factors may also disrupt or destroy many ecological interactions between other organisms and migratory birds, such as between plants and pollinators or seed dispersers [107]. Climate-change-related disruptions in these ecological interactions may also affect time stress, by affecting the optimal timing of a migrant’s behaviour. Appropriate timing of arrival at the breeding grounds is widely considered to significantly affect a bird’s fitness [108]. This is particularly true for high-latitude breeders where the short summer period provides a very limited window of opportunity, especially for large birds, which require more time for egg production, incubation and growth than small birds [29]. Thus, careful scheduling of nutrient-demanding reproductive activities to match the phenology of potential food sources confers significant fitness benefits. Careful timing of the initiation of migration may also be crucial for birds to move across the globe on the wave of advancing spring. For Arctic breeding waterfowl, their ability to predict the occurrence of this ‘green wave’ has been hypothesized to be an important prerequisite for their successful migration [109]. On the other hand, some large birds may carry extra energy and nutrient reserves acquired during migration to their breeding grounds, and use this capital to initiate breeding activities well before the food peak at the breeding grounds. This gives them a head start for breeding and allows them to better exploit local resources when the nutrient demands of their hatched young are at their peak [110].

Inconsistent changes in climate variation along a migration route may disrupt the existing spatial patterns in the phenology of food sources that migrants rely upon. For various European-breeding trans-Sahara migrants, uncoupling of the timing of resources along the flyway has been hypothesized to be one of the major reasons for their decline [111]. Modification of migratory and subsequent breeding schedules in attempts to match climate-change-driven changes in food availability along the flyway has been observed in geese and numerous passerine species; however, these adjustments in timing appear to be imperfect [111]. Although some theoretical modelling of optimal migration itineraries of birds in response to a changing environment indicate that migrants may theoretically be able to cope with substantial changes to their surroundings [112], this has only been partly confirmed by empirical data [113]. The outcome of those theoretical models may not appear surprising given the huge climatic changes that many of the current migratory avifauna experienced during the past ice ages. However, it should be borne in mind that during those periods, some species experienced bottlenecks that almost led to their extinction [114]. Theoretical models also indicate that abrupt changes in environmental conditions may be too rapid for birds to cope with, unless transitions are in temporal synchrony with birds’ ability to evolve or adapt to these changes [112]. Moreover, optimality models consider only what a bird should and should not do, and assume it has the mechanisms to make appropriate responses. Importantly, potential physiological conflicts in the progression of various life-history stages may occur from the spring migratory stage to breeding and from post-breeding moult to autumn migration, thereby limiting a further compression of these processes in time [115–117]. Furthermore, timing of migration is primarily under photoperiodic control [118] and, because this ‘zeitgeber’ is not directly coupled to climatic conditions, it may lose reliability under a rapid climate change scenario. In an extreme case, adaptive earlier hatching in response to an artificial early spring led to a maladaptive earlier onset of migration [119]. Adaptations to changes in the timing of spring phenology may thus be constrained by entrainment of associated physiological mechanisms. Environmental conditions such as food
availability [120], ambient temperature and pressure [121], and geomagnetic field [122] also appear to affect the motivation for increased rates of feeding and the timing of migration, but further insight into the relative importance of these factors is needed before predictions of a given species’ resilience to climate change can be reasonably made. A mechanistic model that reliably predicts the timing of migratory behaviours is certainly of paramount importance [123].

5. Future Directions

(a) Empirical data and predictive modelling

The behavioural and physiological traits that enable migratory species to exploit geographically disparate habitats are believed by some to make them less vulnerable to global change processes than their sedentary counterparts [124], but this conclusion is not supported by empirical data [12,13]. Although migratory traits potentially allow individuals to escape unfavourable conditions (cf. Loehle [39]), accumulating evidence indicates that long-distance migrants are particularly vulnerable to current environmental changes. Clearly, there is a great need to produce informed predictions on the potential effects of global change processes on biota, including migrants. We have identified a range of potential factors by which global change may negatively impact on the fuelling rate, body stores and vitality of migratory birds. In the majority of cases, the evidence we present comes from studies conducted in non-avian or non-migratory taxa and only indirectly relate to assessing the effects of global change. There is clearly a pressing need for physiologists to: (i) reconcile the empirical and theoretical studies on the physiology of avian flight such that accurate predictions can be made on the body stores needed to accomplish migratory flight in a range of environmental conditions, particularly at altitudes used by migrants; (ii) improve our understanding of the impact of food quality, diseases and toxicants on the fuelling rate, flight performance and vitality of migratory birds, and the physiological underpinnings of these impacts (notably for disease and toxicants); and (iii) use mechanistic models that integrate the various known abiotic and biotic factors that determine the timing and extent of migratory behaviours, in order to predict the behaviour of migratory birds under a range of global change scenarios.

For the reconciliation of empirical findings with theoretical models on the physiology of avian flight, including consideration of bird flight under high-altitude conditions, the construction of a hypobaric wind tunnel [89] and advancements in logging physiological data during flight and migration [125–127] are exciting developments. In the light of the potentially increased environmental challenges imposed upon migrants, emerging data are of great importance in determining the maximum capacity of flight endurance for long-distance migrants.

The capacity of particular species to make appropriate behavioural and physiological adjustments to global change effects depends importantly on their genetic variation in key ecologically relevant traits as well as their phenotypic flexibility [128], which together also determine the timescale of an adaptive response [129]. In this regard, species with short generation times are believed to have more capacity to evolve at rates better matching current rates of global change than those with longer generation times [130]. This is likely to make long-living migratory species with low fecundity more vulnerable to rapidly changing environmental conditions than those having a more rapid pace of life. On the other hand, longer-lived species are known to have higher cognitive abilities than birds with shorter lifespans [131]. Thus, the reduced rate of evolutionary adaptation associated with long generation intervals may be offset by these species having a greater potential for extended learning periods that support experience-based adjustments to environmental perturbations. Species are also likely to differ in their capacity for phenotypic adjustment to global change processes. This may allow many species to attain sufficient reproductive capacity under changed conditions to permit selective forces to favour offspring with the most appropriate genotypes and, thus, permit local adaptation. Sometimes the phenotypic adjustments that species undertake can lead to unexpected outcomes. Recent studies of range expansion by house finches (Carpodacus mexicanus) have found that the offspring of birds breeding at climate extremes have biased sex ratios. This is due to females initiating incubation soon after the first egg is laid to protect eggs from cold temperatures that result in rises in prolactin, which, in turn, is believed to bias allocation of particular sex chromosomes during meiosis [132]. This emphasizes the importance of better understanding the physiological processes associated with phenotypic and genotypic adjustments in populations displaying changes in migratory behaviour in responses to global change events.

(b) Evaluating vitality

We have discussed how global change hazards potentially affect both the body stores and vitality of migrating birds and have emphasized the limitations of inferring health status from traditional measures of body condition alone. While extent of body stores is highly relevant for predicting the capacity of migrating species to undertake migration and to breed, it must be combined with other physiological measurements to infer health and vitality. The question this begs, however, is how to measure vitality and how such measurements can complement body store quantification to dynamically gauge the health of individuals. We assume that high levels of vitality are associated with resistance to infection and disease, the ability to physically endure energetically demanding activities, the capacity to breed successfully and the ability to maintain appropriate levels of homeostasis over all stages of the life cycle. Because many physiological and morphological traits vary over the annual cycle and differ between species, it is important to establish baseline references for vitality measurements based on a suite of physiologically relevant measurements from a large cohort of individuals judged to be healthy at each key phase of the annual cycle. The measurements selected should be amenable to taking point samples from adults and, in the case of chicks, for repeated measurements where necessary.
The traditional method of inferring health status through estimates of available body stores is particularly problematic for long-distance migrants, because the set-points for these stores changes in an adaptive fashion between migration preparation and other events in the annual cycle. This makes it important to consider other measures to estimate the health and vitality of these birds. Because excursions from homeostasis often provoke the hypothalamic–pituitary–adrenal axis in vertebrates, some insight into an animal’s recent stress history can be gained by determining the dynamic changes in plasma corticosterone from blood samples collected at the moment of capture and at predetermined times afterwards [133]. High levels of circulating corticosterone are associated with emergency life stages and often result in dampened immune capability [134].

Interpretation of these measures is made more complicated by the unknown effects of seasonally variable levels of corticosterone-binding globulin (CBG) on the actual amount of free corticosterone that is circulating and how this affects physiological functions. There is evidence that plasma CBG levels rise disproportionately more than elevations of corticosterone in birds preparing for migration, resulting in less free corticosterone while flying than prior to flight preparation [135]. Traditionally, only free corticosterone was presumed to be biologically active [136–138], but there is increasing evidence that CBG-bound corticosterone may target and selectively release corticosterone at sites undergoing inflammatory reactions [139,140] and may serve as a mechanism for immunomodulation [141]. Thus, both free and total corticosterone should be characterized when establishing vitality indices.

Heat shock proteins (HSPs) are another biomarker of homeostatic perturbance and are less dynamically variable than corticosterone. As is the case for highly elevated corticosterone levels, raised HSP levels have been correlated with lower humoral and cell-mediated immune responses in birds [142] and have also been shown to vary directly with parasite load [143]. Experimental enlargement of clutch size has also been shown to increase HSP levels, presumably in response to the higher stress associated with the increased workload [144]. There is also evidence that HSP levels increase in response to nutritional stress in birds [145]. Because HSP levels vary directly with species longevity [146], it is important to establish baselines for each species of interest at pertinent phases of their annual cycle.

Resistance to disease and infection is best tested by experimentally infecting an individual and measuring its response. This is constrained, however, by both animal welfare and practical considerations. This has prompted use of indirect measures to infer immune capacity such as examining heterophil/lymphocyte (H/L) ratios or determining blood parasite loads. Neither of these measurements gives an accurate assessment of immune capability, however, as parasite load depends on level of exposure to the parasites or their vectors and H/L ratios depend on infection history. This has prompted examination of constitutive immunity and microbiocidal capacity characteristics using blood collected from free-living birds [147,148]. Such measures have been shown to correlate with survivorship in adults and chicks [149,150]. In chicks, measurements of cutaneous swelling a day after injection of phytohaemagglutinin have been shown to predict survival probability [151–153], presumably because this correlates with their disease susceptibility.

The above measurements, and others deemed to reflect measures of vitality, could be evaluated using a multi-dimensional analysis to determine a vitality index for a given individual. These could then be used to assess the distribution of vitality scores among the population at particular points in their life cycle and, through this, evaluate the relative quality of the habitat they are using. For intervals when birds are mobile or using unknown sites while en route to particular destinations, estimates of habitat quality and individual vitality require knowledge of geographical location and how that location affects the individual’s vitality. This requires a simultaneous record of position and a biomarker that reflects its potential effect on the individual. Highly mobile species present a greater challenge to obtain this information due to lack of knowledge of many of their habitat associations. This makes it very important to develop methods that permit identification of habitat use throughout their annual cycle along with identifying potential threats associated with these locations. Such information is very important to identify both populations at risk and where mitigation is needed to offset these risks.

(c) Identifying geographical locations of concern

The miniaturization of electronic devices has advanced rapidly in the past decade, resulting in lightweight light-sensitive geolocators that provide estimates of an individual’s geographical location from the time the unit is attached to the individual until it is recaptured and downloaded. Larger birds can easily carry global positioning system transmitters, which permit dynamic and accurate mapping of their location for extended periods. Estimates of habitat quality might be inferred if habitat use left biomarkers that could be sampled at a later capture site and reliably dated. The best candidates for such sampling are feathers. Many migrants, particularly those breeding at high latitudes, have highly predictable moult schedules. If the phenology of feather replacement is known for a given species and this is combined with knowledge of a bird’s location at the time the feather is being replaced, then it is possible to estimate where birds have been exposed to particular contaminants as well as their level of stress at that time [154–156]. This is because certain metals, organic compounds and circulating corticosterone are incorporated into the developing feather as it emerges from the feather follicle and remain bound to this elongating structure, which serves as an inert, but highly robust, time capsule. If rates of feather growth and timing of each feather’s emergence are known, then an extended timeseries for monitoring pertinent biomarkers is possible [157]. Furthermore, analysis of stable isotopes between feathers and along the length of individual feathers provides another means to estimate geographical location at the time the feathers were formed [158]. Because rate of feather replacement is size-dependent [159], chemical
analysis of feathers from large birds provides an extended window into the quality of the habitats they encounter in their annual cycle.

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