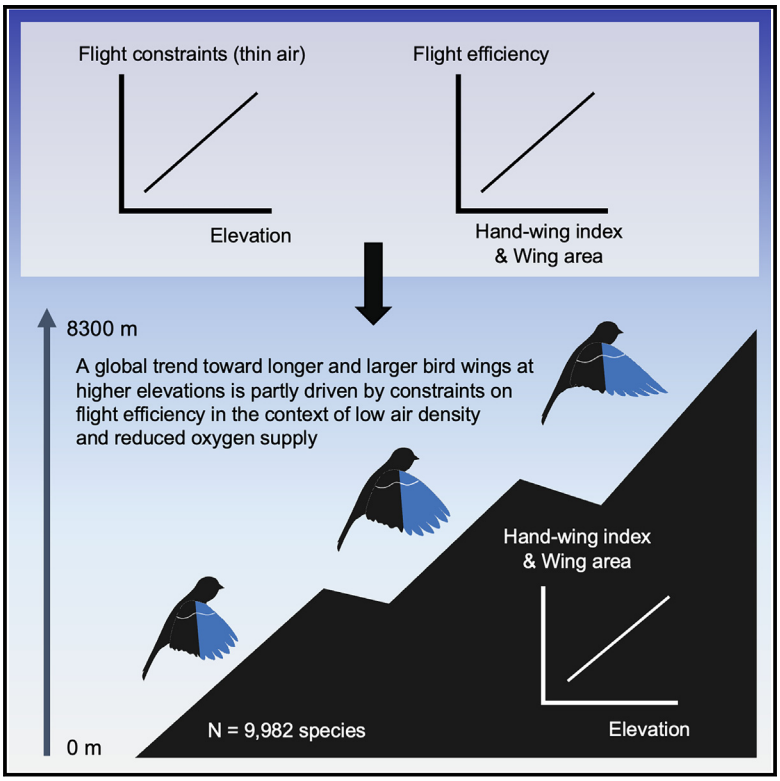
Report

Current Biology

Elevational constraints on flight efficiency shape global gradients in avian wing morphology

Graphical abstract



Highlights

- Low air density at high elevations is thought to reduce flight efficiency in birds
- Phylogenetic analyses confirm elevational gradients in avian wing length and area
- Longer and larger wings may evolve to improve flight efficiency in montane birds
- Air density gradients shape morphological flight adaptations worldwide

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In brief

Yang et al. use morphological trait data from 9,982 bird species to confirm a global gradient in wing length and wing area increasing toward mountaintops, suggesting that low air density constrains flight efficiency at higher elevations, driving the evolution of morphological flight adaptations in montane bird species.

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Report

Elevational constraints on flight efficiency shape global gradients in avian wing morphology

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SUMMARY

Wings with an elongated shape or larger surface area are associated with increased flight efficiency in a wide range of animals from insects to birds.[1–4] Inter- and intra-specific variation in these attributes of wing shape is determined by a range of factors—including foraging ecology, migration, and climatic seasonality[5–8]—all of which may drive latitudinal gradients in wing morphology.[9,10] A separate hypothesis predicts that wing shape should also follow an elevational gradient[5,11] because air density declines with altitude,[12] altering the aerodynamics of flight and driving the evolution of more efficient wings in high-elevation species to compensate for reduced lift.[13–15] Although previous analyses have shown a tendency for longer or larger wings at higher elevations, at least locally,[16–20] it is difficult to rule out a range of alternative explanations since we currently lack a global synthesis of elevational gradients in wing shape for any taxonomic group. In this study, we use phylogenetic models to explore elevational effects on metrics of wing morphology linked to aerodynamic function in 9,982 bird species while simultaneously controlling for multiple climatic factors and ecological attributes of species. We found that relative wing elongation (hand-wing index) and wing area increase with elevation, even when accounting for latitude, temperature seasonality, body mass, habitat, aerial lifestyle, and altitudinal migration. These results confirm a pervasive elevational gradient in avian wing morphology and suggest that aerodynamic constraints linked to air density, perhaps coupled with oxygen deficiency, contribute to global patterns of trait evolution in flying animals.

RESULTS AND DISCUSSION

Morphological adaptations linked to dispersal mediate numerous fundamental processes, including speciation,[21] community assembly,[22] and population-level responses to environmental change.[23–25] The central role of dispersal in many aspects of ecology and evolution has led to increased interest in the mechanisms driving variation in dispersal ability and the extent to which they can explain broad geographic patterns in organismal phenotype.[26,27] The most prominent of these patterns is a latitudinal gradient in dispersal ability, driven largely by global climatic gradients and their effect on species ecology.[9,28] In flying animals, this trend is reflected in morphological adaptations for flight efficiency increasing from the equator to the poles,[9,29] a pattern that has also been proposed for elevational gradients, with flight efficiency increasing from lowlands to mountaintops.[15] However, this elevational trend in dispersal-related adaptation has received relatively little attention and potentially arises from a different mechanism linking air density and the physics of flight.[13,30–32]

Average air density decreases almost linearly from sea level to 10 km altitude,[12] gradually increasing constraints on flight efficiency for aircraft and animals alike.[33,34] In animals that rely on flight to forage or move across the landscape, this means that wing morphology adapted to lowland conditions may provide insufficient lift at higher elevations,[13,30] thus driving wing-shape evolution to improve flight efficiency.[5,14,15] Specifically, the "thin-air" hypothesis predicts that wings should increase in elongation or area toward mountaintops[15,16,19] because longer and larger wings can improve energy efficiency or generate increased lift, respectively[2,3,30,35] (Figure 1). Despite the clear connection with well-established aerodynamic theory, it is difficult to disentangle the effects of air density from other potential mechanisms, leading to a lack of consensus about the relative role of different drivers of elevational gradients in flight adaptations.[36–39]

The tendency of flying animals to have larger wings at higher elevations was recognized almost a century ago, although the pattern was initially ascribed to a thermoregulatory mechanism, with wing-size differences emerging as a correlate of larger body size, in accordance with Bergmann's rule.[40,41] In birds, a different set of hypotheses has emerged predicting elevational gradients in wing size or loading driven by ecological factors,

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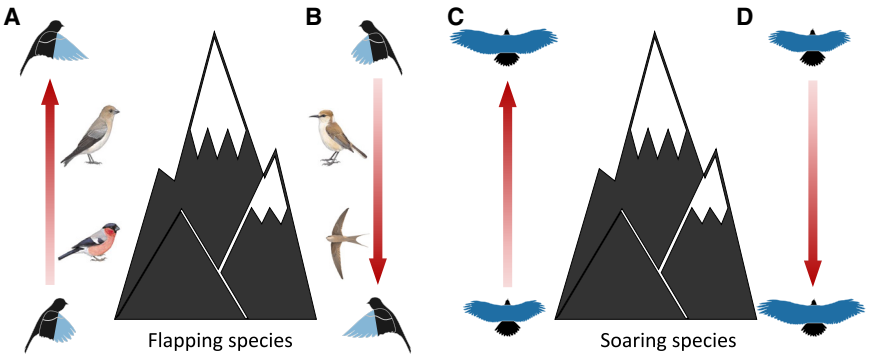

Figure 1. Potential direction and drivers of elevational gradients in avian wing morphology

(A) Air density and oxygen supply decline with elevation from 0 to 10 km above sea level. Given that elongated wings are associated with improved flight efficiency, flapping species living at higher elevations (e.g., *Carpodacus sillemi*) may evolve longer and more pointed wings than lowland relatives (e.g., *Pyrrhula pyrrhula*) to provide greater lift or improved flight efficiency in lower density air.

(B) Any elevational trend related to air density and oxygen supply may be altered or reversed in macro-scale comparative analyses because overall gradients in flight adaptations may reflect foraging ecology, lifestyle, or seasonal mobility (Figure S1). For example, mountaintops are colder with more open habitats and fewer flying insects; thus, a higher proportion of montane species (or trophic guilds) may be terrestrial (e.g., ground tit), whereas lowlands are warmer with more flying insects, increasing the diversity of aerial insectivores (e.g., *Cypsiurus parvus*).

(C) Similarly, in soaring species, larger or more elongated wings may evolve at higher elevations to compensate for lower air density and maintain flight efficiency.

(D) Alternatively, the wing area gradient may be reversed in macro-scale comparative analyses because higher temperatures and associated thermal uplifts increase the size and diversity of soaring species at lower elevations. Red arrows show opposing elevational gradients—between lowlands and mountaintops—of wing length, hand-wing index (HWI), and hand-wing area (HWA). Bird images are reproduced with permission from Birds of the World (Cornell Lab of Ornithology) and Lynx Nature Books (see acknowledgments).

such as adaptation for mobility in open landscapes and to avoid harsh winter climates in high mountains.[17,42] Early studies also speculated that lower air density could reinforce this effect.[5,11] For example, based on anecdotal observations of museum specimens, Erwin Stresemann[43] proposed that wings of highland bird species were longer and more pointed to compensate for the reduced "carrying capacity" of the air, even in sedentary species. Recent quantitative analyses have tested variants of this hypothesis in a range of taxa, with some showing evidence of increased wing size or elongation at higher elevations for particular bird species,[16,20,44–46] and other studies finding no such relationship.[42,47,48] Similarly, in some groups of insects, wing size appears to increase in relation to body size at high elevations,[19,39] whereas other studies show the opposite trend of wing reduction.[49,50]

These opposing trends may reflect variation among species in the effects of ecological gradients linked to climate, food supply, or oxygen deficiency. For example, some insect species are thought to become less aerial and shorter-winged at high elevations because lower temperatures and stronger winds increase the cost and risk of flight.[49,50] In birds, too, the proportion of aerial-foraging species may decline at higher elevations, either because cooler temperatures reduce the availability of airborne insect prey[51] or limit the production of thermal updraughts used by soaring species.[52] In broad-scale comparative analyses, differences in species ecology may therefore reverse the overall pattern of wing elongation or enlargement at higher elevations in some contexts (Figure 1), complicating elevational trends in phenotype. Another factor to be considered is the reduced concentration of atmospheric oxygen at high elevations, potentially exacerbating the effects of lower air density and increasing the metabolic cost of inefficient wing shape for species with energetic flight styles.[32,53] Conversely, physiological constraints on flight efficiency are substantially relaxed in species with passive flight styles (e.g., gliding or soaring).[54]

In the most detailed study to date, Youngflesh et al.[20] found that intra-specific variation in relative wing length increased with elevation in 105 North American bird species (mostly passerines). This pattern is consistent with the thin-air hypothesis, providing valuable insights from a microevolutionary perspective. However, the conclusions may be undermined by two potential sources of uncertainty. First, wing length is not explicitly linked to wing-aspect ratio or lift-to-drag ratio and is therefore only weakly related to flight efficiency.[1,55,56] Second, an array of alternative factors could generate similar patterns, most importantly the tendency toward greater local or seasonal mobility of birds near mountaintops, particularly in the temperate zone.[57–59] All data used by Youngflesh et al.[20] were sampled >25° latitude, where most high-elevation passerines (populations or species) routinely undertake altitudinal movements to avoid harsh winters[60,61] (Figure S1). Since migratory tendency often varies within passerine species in the temperate zone, populations breeding at higher elevations may be under stronger selection for seasonal movements than populations residing at lower elevations. This trend is well known in several common North American species,[60,61] including largely or partially migratory forms, such as American Robin (*Turdus migratorius*)[62] and Song Sparrow (*Melospiza melodia*).[63] Efforts to disentangle aerodynamic mechanisms from migratory tendency therefore face a critical challenge that can only be met through concurrent testing of alternative hypotheses, using data sampled across a wider span of geographical and ecological contexts.

To assess the generality and underlying drivers of gradients in wing morphology, we compiled a dataset of elevational ranges for all extant birds (n = 9,982 species) and then used phylogenetic models to test whether the maximum elevation at which bird species occur predicts their relative wing elongation and wing area. Birds offer an ideal opportunity to test the thin-air hypothesis as they populate the entire elevational range habitable to terrestrial vertebrates from below sea level to at least 8.3 km altitude. Crucially, the global sample of birds includes many species (n = 369) with elevational ranges extending >4 km above sea level and latitudinal ranges centered on tropical and sub-tropical mountains (<30° latitude; Figure S1). These include some of the world's most sedentary bird families, including tapaculos

(Rhinocryptidae) and antpittas (Grallaridae). By including these and many other sedentary tropical montane species,[64] our analysis can better differentiate elevational patterns from migratory tendency. In addition, the aerodynamic properties of bird flight can be quantified using published morphological trait data[65] to calculate relevant metrics, including hand-wing index (HWI) and hand-wing area (HWA).[1,9,66,67] HWI—a measure of wing pointedness or elongation correlated with wing-aspect ratio[56,68]—is calculated from the lengths of the wing chord and the first secondary feather, which indicate wing length and wing width, respectively[9,35] (Figures S2A and S2C). Using the same variables, we also adapted a method proposed by Wright et al.[66] to compile a dataset of HWA for all birds. Although HWA quantifies the area of the outer wing only,[55] we show that it is highly correlated with the aeronautical wing area—the total area of the underside of both wings plus the intervening body[30] (see STAR Methods; Figures S2B and S2D). Therefore, increased HWI is associated with greater energetic efficiency of flight,[1,69] while increased HWA indicates greater aerodynamic lift.[16,30]

Since the influence of air density on HWI and HWA may vary according to flight style[30,54,70] (Figure 1), we divide birds into groups that primarily use flapping flight (n = 9,559 species) and soaring flight (n = 378 species). In combination, these datasets allow us to assess the impact of elevation on wing morphology in the context of multiple factors known to shape wing evolution, including body mass,[54,71] metabolic costs,[53,54,70] aerial lifestyle,[1] migration,[6,28] and trophic niche,[71,72] as well as environmental variables such as latitude,[9] temperature seasonality,[5,9] and habitat openness[5,17] (see STAR Methods). Thus, although it is not possible to directly test the impact of thinner air on flight adaptation at this scale, our analyses are able to disentangle the likely contribution of air density from other critical factors, many of which vary with elevation.

Elevational gradients in avian wing morphology

Globally, we found that soaring birds are generally restricted to lower elevations and have more pointed and larger wings relative to body mass, compared with flapping species (Figures 2A and 2B). In both cases, soaring and flapping species show an overall increase in relative HWI and HWA as elevation increases, especially >4 km above sea level. However, there are prominent differences at low elevations, with soaring species showing a dramatic decrease in HWI and increase in HWA up to around 2 km above sea level (Figures 2A and 2B). This pattern is primarily driven by a subset of seabirds—including albatrosses and petrels—with dynamic soaring flight associated with extremely long and narrow wings.[73] Unlike thermal soaring, dynamic soaring relies on strong winds and is largely restricted to marine environments at the lowest elevations (see STAR Methods). When seabirds (n = 110 species) are removed, soaring and flapping land birds show similar gradual increases in HWI and HWA with elevation, consistent with predictions of the thin-air hypothesis (Figures 2A and 2B). These elevational patterns are further corroborated by significant positive gradients in average HWI and HWA when all species (including seabirds) are partitioned into elevational bands based on their distribution (Figures 2C and 2D).

The global-scale correlation between elevation and wing shape may be at least partly explained by factors other than air density. To tease apart the contribution of potential alternative mechanisms, we ran a set of phylogenetic generalized least square (PGLS) models to test the effect of elevation while controlling for eight major determinants of wing morphology (latitude, temperature seasonality, habitat openness, body mass, flight mode, aerial lifestyle, migration, and diet). Even when accounting for the combined contribution of all these factors, we found that elevation remained significantly positively correlated with both HWI (95% confidence interval [CI] = [0.002, 0.015], $p_t < 0.01$) and HWA (95% CI = [0.014, 0.021], $p_t < 0.001$; Figure 3; Table S1) in models containing all volant bird species (n = 9,788). To assess whether these results were driven by special cases, we removed two problematic subsets of species, namely seabirds because of their use of dynamic soaring[73] and long-distance migrants, which potentially occur outside their optimal range as vagrants or fly at extreme altitudes during migration[74,75] (see STAR Methods). When we restricted our sampling to non-migratory land birds (n = 8,703 species), the effect of elevation remained similar for HWA and increased for HWI (95% CI = [0.005, 0.018], $p_t < 0.001$; Table S1), supporting our all-species models (Figures 3A and 3B).

Perhaps the most obvious factor confounding tests of the thin-air hypothesis is the greater mobility of montane species, particularly in the temperate and boreal zones (Figure S1), where high elevations are seasonally inhospitable.[57–59] At these latitudes (>30°), montane bird species such as *Leucosticte* rosy-finches in the Rockies and *Carpodacus* rosefinches in the Himalayas (Figure 1) may be long-winged to meet the physiological demands of irruptive cold-weather movements or altitudinal migration. The results of our multivariate models suggest that the wings of these and other high-elevation species are better adapted for efficient flight than lowland species, even accounting for these migratory habits. Nonetheless, lowland bird species occurring at very high latitudes often have relatively long wings because of their mobile lifestyle in winter (Figure 3C), suggesting that the elongated wings of high-elevation species may reflect an overlooked gradient toward seasonal mobility in species scored as residents or short-distance migrants.

To examine this question, we compared wing morphology of species living at low latitude (<30°) and high elevation (>4 km) with species in the same family living at high latitude (>30°) and low elevation (<3 km; see STAR Methods). Both groups may be adapted to periodic movements during harsh climatic conditions, yet they experience contrasting air density. Note that many tropical montane lineages are excluded from this comparison because they lack high-latitude relatives, leaving only 14 families with enough representatives in each group (see STAR Methods). In this sample, we found that tropical montane species exposed to thin air have roughly similar HWI (paired t test, 95% CI = [−0.209, 0.047], p_t = 0.19) and consistently higher HWA (95% CI = [0.034, 0.154], $p_t < 0.01$) than temperate lowland species exposed to dense air (Figures 3D and 3E; Figure S3). It is worth emphasizing that high-latitude species tend to experience much stronger seasonality, requiring greater mobility in winter, than tropical montane species. Thus, the fact that average wing elongation and wing area in tropical birds is nonetheless roughly similar to or significantly larger than their high-latitude relatives

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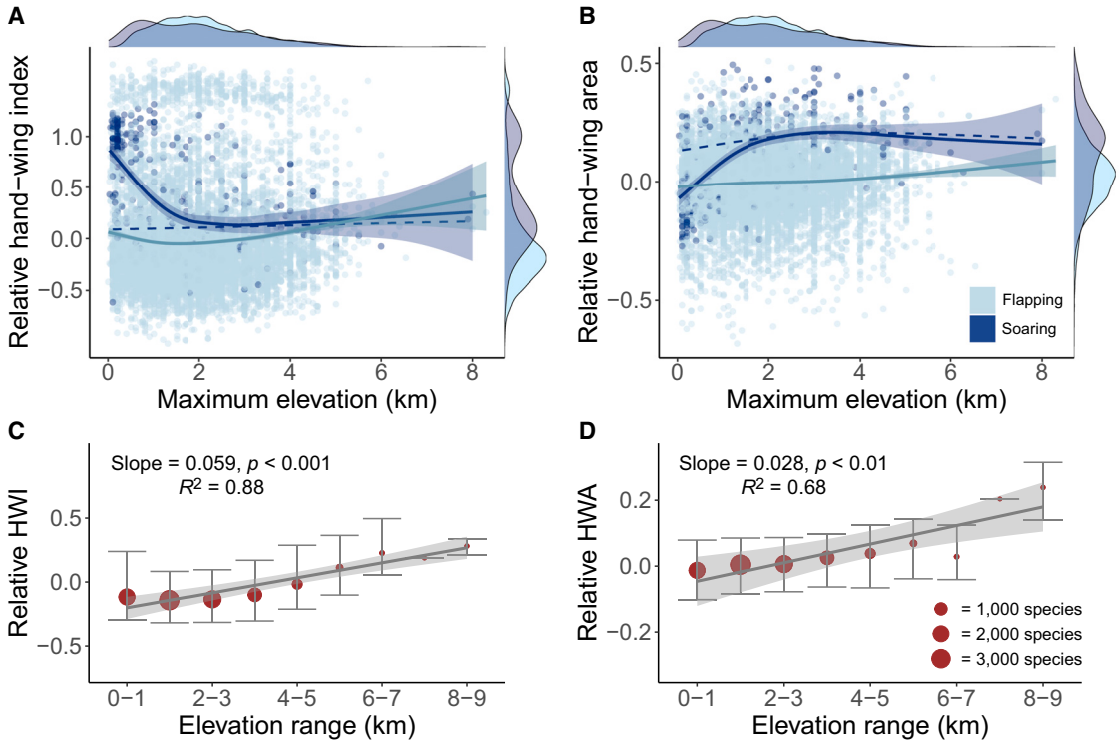

Figure 2. Relationship between wing morphology and elevation in birds

(A) In 9,559 species with flapping flight, hand-wing index (HWI) increases with maximum elevation (i.e., the highest elevation reported for each species). In a smaller sample (n = 378) of soaring species, HWI initially declines sharply with elevation under 2 km and then increases at higher elevations. However, high HWI in low-elevation species is largely driven by narrow-winged seabirds, in which soaring is often wind-assisted and therefore less constrained by air density. After removing seabirds (see STAR Methods), soaring species show a more gradual increase in HWI with elevation (dotted line).

(B) Hand-wing area (HWA) of flapping and soaring species also increases with elevation. When seabirds are removed (dotted line), HWA of terrestrial soaring species increases gradually up to 4 km, then levels off at the highest elevations. (A and B) Density plots adjacent to panels show the overall distribution of flapping and soaring species across axes of elevation and wing morphology.

(C and D) Both relative HWI and HWA increase with elevation when flapping and soaring birds are grouped into 1 km-wide elevational bands based on their maximum elevation. Central dots show median wing measurements for each elevational band, whiskers show first and third quartiles, and dot size represents the sample size within each elevational band (1–3,381 species). Statistics shown are from a linear regression (gray line) between median HWI (C) or HWA (D) and max elevation, and the shaded area shows a 95% CI. All analyses use relative wing measurements (HWI or HWA corrected for body size) calculated as the residuals from linear models between standardized wing measurements and body mass. HWA and body mass were log-transformed before standardization.

provides strong evidence that adaptations for flight efficiency can evolve in response to thinner air rather than mobile lifestyles alone.

At a global scale, in accordance with Bergmann's rule, we found that avian body mass increases gradually with elevation (see STAR Methods; Table S2). This could imply that increased wing elongation and wing area in montane species simply reflect an increased body size, in line with some previous claims.[40,41] However, our results reject this hypothesis. When we removed body mass from model predictors to examine wing changes without size correction, we detected stronger positive effects of elevation on most wing metrics (Tables S1 and S3; Figure S4A). More importantly, our multivariate models confirm positive elevational gradients of wing area and elongation after accounting for body mass. Taken together, these findings confirm that birds living at higher elevations have longer and larger wings, on both absolute and relative scales, supporting the view that montane environments have general and consistent effects on the evolution of flight adaptations.

In soaring species (n = 378), the direction of morphological responses to elevation was less clear. Overall, their HWI decreased with maximum elevation (95% CI = [−0.067, −0.002], p_t < 0.05), while HWA increased (95% CI = [0.010, 0.045], p_t < 0.01; Table S1). However, these results are again driven by marine species. When we removed all seabirds from the sample, both HWI (95% CI = [−0.043, 0.040]) and HWA (95% CI = [−0.007, 0.040]) were no longer associated with elevation (Table S1). These weak effects may simply reflect a much smaller sample size, particularly for non-marine soaring species (n = 268). Alternatively, divergent responses between flapping and soaring birds may be caused by their fundamentally different sources of lift during flight. Most non-marine species soar by generating lift from thermal convection currents, which are largely determined by temperature rather than air density.[52,54] In addition, a weaker link between air density and wing morphology in soaring species at high elevations may arise because they rely on upwash—i.e., winds pushed upward by topographical features including slopes and cliffs[76]—or because

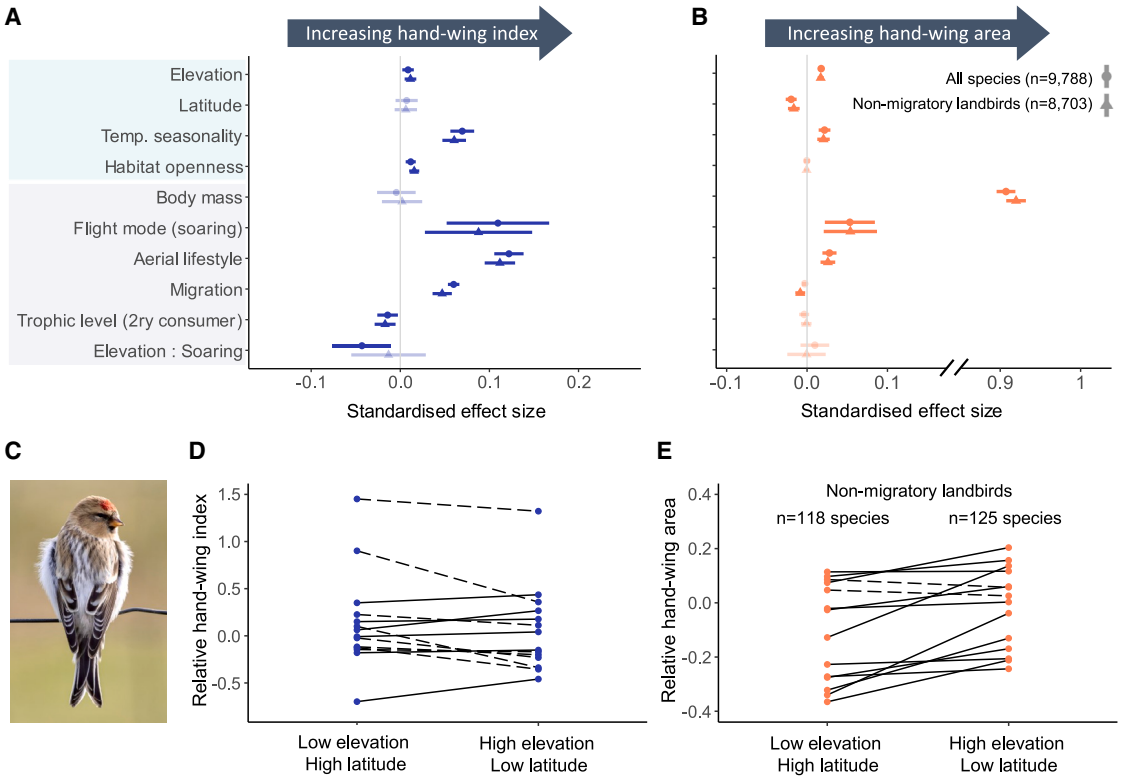

Figure 3. Elevation predicts avian wing morphology

(A and B) Forest plots show parameter estimates of phylogenetic models testing effects of environmental factors (blue box) and species traits (mauve box) on (A) hand-wing index (HWI) and (B) hand-wing area (HWA). Points show the mean, and error bars show 95% CI. Positive values indicate a positive correlation between the predictor and the corresponding wing metric. Seabirds and long-distance migrants may be under different selection pressures (see STAR Methods), so we repeated models with both these categories removed. Results shown are therefore based on all volant birds (dots) and the subset of non-migratory land birds (triangles). Significant effects are inferred when estimated 95% CI does not span zero (highlighted in a darker shade).

(C) Larger and more elongated wings often characterize non-migratory species of high latitudes and low elevations, such as the Arctic Redpoll (*Acanthis flammea hornemanni*), suggesting that strong selection for dispersal or mobility associated with avoiding harsh climatic conditions can drive increases in HWI and HWA even when air density and oxygen supply are high (photo: Daniel Gornall).

(D and E) To test whether similar climatic conditions >4 km above sea level explain elevational gradients in wing morphology, we compared average HWI (D) and HWA (E) in lowland species restricted to high latitude with highland species restricted to low latitude, within avian families (see Figure S3 for sampling details). Results show that the highest HWI and HWA are most often associated with high elevation (solid lines) rather than high latitude (dashed lines). Calculation of relative wing metrics follows the procedure described in Figure 2. Temp., temperature; 2ry consumer, secondary consumer. See Tables S1–S3 for details of phylogenetic model results.

they use other adaptations to improve lift,[77] including respiratory air sacs.[78]

A steepening of morphological gradients toward mountaintops

Although our models reveal global trends in wing morphology across the entire elevational gradient, they provide limited insight into how these trends vary with elevation. To explore the finer-scale and potentially non-linear relationship between wing morphology and elevation (Figure 2), we used a "sliding-window" approach to divide our sample into a series of subsets based on species' maximum elevation (0–3 km, 1–4 km, and so on), then repeated PGLS models within each elevational band, accounting for the same set of climatic and ecological factors (see STAR Methods). These "sliding-window" models revealed that positive correlations between elevation and nearly all wing metrics gradually strengthened as elevation increased, with particularly strong effects over 4 km above sea level (Figure 4). For example, the effect of maximum elevation on HWI is weak or non-significant in the lowest five elevational bands and jumps to a strong effect (0.126; 95% CI = [0.017, 0.236], $p_t < 0.05$) in the highest elevational band. The findings are also robust to the removal of seabirds and long-distance migrants, as well as using alternative methods of dividing the sample (see STAR Methods; Figure S4).

This steepening gradient suggests that avian wing morphology is more sensitive to elevational change at the highest elevations inhabited by birds, matching observations of very long-winged species resident year-round >5 km, e.g., some *Muscisaxicola* ground tyrants in the Andes.[62] These cases are most likely evolutionary responses to reduced flight performance at high elevations, which in turn appears to be linked to reduced air density, rather than, for example, reduced oxygen availability.[34] Nonetheless, hypoxia may be a contributory factor increasing the negative impact of lower air density at high altitude,[15,19] thereby accentuating selection for optimal flight efficiency.[32,53]

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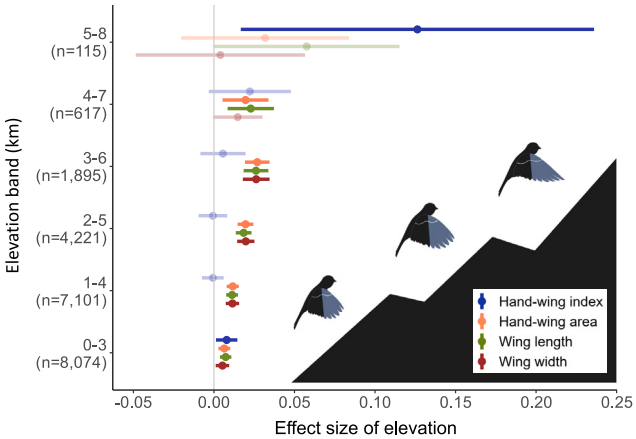

Figure 4. Gradients in avian wing morphology are accentuated at the highest elevations

Forest plot shows the parameter estimates of maximum elevation on wing morphology, based on separate phylogenetic models for each 3-km-wide elevational band (starting with 0–3 km and ending with 5–8 km above sea level). The sample sizes within elevational bands refer to flapping species only because the models included an interaction term (elevation: flight mode) such that the main effect of elevation was estimated with flight mode at the reference level. Central points show the mean, and error bars show 95% CI. Results were generated using 100 randomly selected trees and averaged via Rubin's rules. Positive values indicate the strength of positive correlation between maximum elevation and the corresponding wing metric. Significant effects are inferred when estimated 95% CI does not span zero (highlighted in a darker shade). The findings were robust to the removal of seabirds and long-distance migrants and the use of alternative bandwidths (2 and 4 km; Figure S4). Models testing the absolute changes in wing morphology (without size correction) showed similar trends with larger effect sizes (Figure S4). Silhouettes illustrate tendency of wings to become larger and more elongated with increasing elevation.

To obtain further insights into adaptive mechanisms, we decomposed our flight efficiency metrics into their underlying variables: wing length and wing width (Figure S2). In both cases, the global PGLS models showed a significant positive relationship with elevation (Table S3). In other words, increasing elevation is not simply associated with wing elongation but also with an increase in wing width, helping to explain why the effects of elevation are not restricted to HWI (an index of elongation) and more strongly predict the gradient in HWA (which reflects a combination of wing length and width; Table S1). A closer inspection of elevational gradients in these traits reveals that wing length and wing width both increase at similar rates for the first 4–5 km above sea level, after which the slope in wing width flattens while the slope in wing length increases (Figure 4). This helps to explain the abrupt increase in HWI at extremely high elevations.

Implications and applications

Indices of flight efficiency (e.g., HWI) are often assumed to reflect dispersal ability or dispersal limitation in birds.[9,24,66,67] While this assumption is likely to be robust in macroecological studies,[1] our findings suggest a potential decoupling of wing shape and dispersal ability at high elevations. That is, the prominent increase in HWI or wing area at mountaintops may reflect a compensatory adaptation that maintains the same levels of aerodynamic capacity without translating into increased flight efficiency or dispersal ability. Variation in wing shape should therefore be used with caution as a proxy for these traits, particularly when sampling across broad elevational gradients. For example, analyses using avian HWI as an index of flight efficiency should consider accounting for elevational effects using global datasets of avian elevational ranges presented in this study (Dataset 1). To maximize the utility of elevational data in future research, we present them under two alternative taxonomic treatments (see STAR Methods).

Our results may also have implications for understanding and predicting responses of montane biodiversity to climate change. Global warming has long been known to drive upslope movement of animals,[79] with dispersal ability being a critical factor determining the rate and extent of elevational shifts to cooler montane refugia.[80] A growing number of studies have explored the behavioral and physiological challenges facing lowland species tracking their climate niches upslope,[81,82] particularly in the tropics.[83,84] Previous analyses have highlighted a range of obstacles to life at high elevations, including competitive interactions,[85,86] impaired breeding, and metabolic inefficiency.[57,87,88] Our findings add a further dimension to these challenges, suggesting that aerodynamic factors will increase flight costs for lowland-adapted animals moving upslope in response to increasing temperature. Similar constraints may help to explain the counter-intuitive findings of a previous study showing that flying insects are slower, rather than faster, to shift upslope due to the higher aerobic demands of flight, exacerbated by lower air density.[89]

Limitations and future directions

A few factors should be borne in mind when interpreting our results. For example, the behavior of many bird species is poorly known, particularly in the tropics,[90] increasing uncertainty around our classification of flight behavior, especially aerial lifestyle. In addition, we use the maximum elevation for each species, which has many advantages (see STAR Methods) but may be more sensitive to sampling effort and potentially overemphasizes extreme conditions that are not experienced by most individuals. To explore these issues, we scored data uncertainty using standard techniques[91] and calculated mean elevations for each species (see STAR Methods). When we reran all models restricting the sample to high-certainty data (n = 6,854 species) or replacing maximum elevation with mean elevation (n = 9,788 species), the results were largely unchanged (Tables S1 and S3; Figure S4). The relationship between elevation and HWI was slightly weaker using these alternative methods, suggesting that HWI (wing elongation) constrains the maximum elevation reached by birds and is less strongly associated with average elevation. The correlation between elevation and all other wing metrics (wing area, length, and width) remained the same (Tables S1 and S3), supporting our main conclusions.

After accounting for a range of contributory factors, the absolute effect of elevation on wing morphology in our models was relatively small (Figure 3). Although small effect sizes are the norm in global multivariate analyses, they may seem surprising in this case given that air density declines by >65% from sea level to 10 km altitude.[12] The effect of this decline on wing shape may

be reduced by other flight adaptations evolving in response to low air density and hypoxia.[32,53] For example, aerial buoyancy can be aided by concealed air sacs in soaring birds,[78] while all flying animals can theoretically improve flight efficiency in thin air by adjusting the "angle of attack" in their wing movements,[76,92] altering flight speed and trajectory,[13,93] or morphing wing shape during flight to achieve higher maneuverability.[76,94] Such behavioral plasticity can reduce the physical and energetic costs of low air density, thereby dampening selection on wing morphology.[92]

The relationship between elevation and wing evolution could also be complicated by a suite of other physical properties known to influence flight performance, including temperature, humidity, and wind speed.[15] While average air density decreases almost linearly across the altitudes relevant to avian flight,[12] air density itself is influenced by temperature and humidity and thus may partially decouple from altitude, giving rise to the concept of "density altitude" in aeronautics.[95] In addition, wind speed generally increases with altitude,[15] potentially compensating for the decline in air density because lift is proportional to wind speed.[13] To date, most aerodynamic models are designed to describe stable or gliding flight paths, while living organisms need to optimize flight during various stages (e.g., take-off[54] and landing[96]) as well as complex atmospheric conditions.[97,98]

The fact that elevational gradients in HWI and HWA are statistically detectable at global scales despite these varied sources of noise and non-linearity suggests that elevational constraints on flight efficiency have a consistent effect. However, a thorough understanding of the impact of air density on animal flight adaptations requires the development of more refined aerodynamic models, along with a consideration of multiple alternative pathways by which birds can accentuate the support and thrust provided by the wings in flight.[76] Finally, experimental manipulations of atmospheric properties and wing morphology in a sample of different organisms may provide a more rigorous test of the thin-air hypothesis and associated ideas.

Conclusions

Previous research has confirmed that a latitudinal gradient in avian wing morphology is driven largely by ecological adaptations to climatic seasonality at higher latitudes, including accentuated dispersal ability and migration as strategies to cope with seasonal fluctuations in resources.[6,9,28] Our analyses reveal that adaptations to promote flight efficiency also follow a consistent elevational gradient at a global scale, with both wing elongation and area increasing toward mountaintops. This pattern persists even when we account for a wide range of climatic and ecological factors predicted to shape avian wing morphology. We therefore provide compelling support for the thin-air hypothesis, particularly given the steep gradient in wing length detected at the highest elevations reached by birds, where a combination of lower air density and reduced atmospheric oxygen may exert stronger selection for greater lift or flight efficiency. More broadly, our findings highlight the potential role of aerodynamic constraints as a general mechanism driving wing evolution in flying animals and limiting their capacity to undergo rapid range shifts to higher elevations.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Joseph Tobias (j.tobias@imperial.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data used in this study, including new datasets of wing area, aerial lifestyle scores, and elevational ranges for all bird species, have been deposited in an online repository where they are publicly available (Dataset 1 at https://doi.org/10.6084/m9.figshare.28477148).
- Code for reproducing all analyses is available at https://doi.org/10.6084/m9.figshare.28477148 and https://github.com/jingyii-yang/Avian-wings-Elevational-gradients.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, J.A.T. and A.C.L.; data collection and curation, J.Y., C.Y., H.-w.L., and J.A.T.; formal analysis, J.Y.; funding acquisition, J.A.T.; investigation, J.Y., C.Y., H.-w.L., and J.A.T.; methodology, J.Y. and J.A.T.; project administration, J.Y. and J.A.T.; supervision, J.A.T.; visualization, J.Y. and J.A.T.; writing – original draft, J.Y. and J.A.T.; writing – review & editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Linear measurements of wing morphology	AVONET[65]	https://figshare.com/s/b990722d72a26b5bfead
Elevation	del Hoyo[99]; White and Bennett[100]; Quintero and Jetz[101]; see Dataset 1 for details	https://doi.org/10.6084/m9.figshare.28477148
Temperature seasonality	CHELSA[102]	https://chelsa-climate.org/downloads/
Species distribution maps	BirdLife International and Handbook of the Birds of the World[103]	http://datazone.birdlife.org/species/requestdis
Temperature seasonality extracted from species distributions; flight mode	This study	https://doi.org/10.6084/m9.figshare.28477148
Aerial lifestyle index	This study; Weeks et al.[1]	https://doi.org/10.6084/m9.figshare.28477148
Centroid latitude; habitat openness; body mass; migration; trophic level	AVONET[65]	https://figshare.com/s/b990722d72a26b5bfead
Avian global phylogeny	BirdTree[104]	https://birdtree.org/
Software and algorithms		
R v.4.2.2	R Core Team[105]	https://www.r-project.org/
Ape	Paradis and Schliep[106]	https://cran.r-project.org/web/packages/ape/
Caper	Orme et al.[107]	https://cran.r-project.org/web/packages/caper/
Tidyverse	Wickham et al.[108]	https://tidyverse.tidyverse.org/
PBSmapping	Schnute et al.[109]	https://cran.r-project.org/web/packages/PBSmapping/
Raster	Hijmans[110]	https://rspatial.org/raster/
Phylolm	Ho and Ané[111]	https://cran.r-project.org/web/packages/phylolm/
Mice	van Buuren and Groothuis-Oudshoorn[112]	https://github.com/amices/mice

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Morphological trait data

To quantify interspecific variation in wing morphology related to flight ability, we used two metrics: hand-wing index (HWI) and hand-wing area (HWA). We extracted HWI from global datasets[9,65] that calculated the index from two wing measurements – wing length (WL) and secondary length (SL) – as (WL-SL) / WL x 100 following Claramunt et al.[21] (Figure S2A). HWI describes the pointedness or elongation of the wing, as opposed to wing length; e.g. hummingbirds (Trochilidae) have relatively short wings with high HWI whereas trumpeters (Psophidae) have relatively long wings with low HWI. Wing length alone is therefore uninformative about flight ability, whereas HWI is thought to provide an index of wing-aspect ratio[56,68] and thus often proposed to reflect both flight efficiency and dispersal ability.[1,9,21,69]

The connection between wing aspect ratio and flight efficiency in birds is well-supported by aerodynamic theory[14,30] and empirical studies.[113,114] However, estimates of aspect ratio are relatively scarce whereas HWI is available for all bird species.[9,65] To test whether HWI reflects variation in aspect ratio for a diverse sample, we compiled wingspan and wing area data for 711 bird species (Dataet 1B) and calculated their aspect ratio as wingspan^2/wing area following Pennycuick.[30] Our analysis confirmed a strong association (Pearson's correlation = 0.83, Figure S2C), supporting the use of avian HWI as an index of flight efficiency. Species averages for HWI, WL and SL were obtained from the AVONET dataset[65] (n = 9,982 species) wherein most estimates are based on samples of at least four museum specimens per species, or inferred from closely related species with similar morphology. Inference was required in only 45 species (0.5% of the sample) lacking measurements for one or more traits, and the identity of surrogate species is provided in AVONET.[65]

No global datasets of avian wing area currently exist, so we calculated a standardised index of wing area for all species using WL and SL. Most aerodynamic models[30] define wing area as the total area of the underside of both extended wings plus the underside of the intervening body (Figure S2B). However, we were unable to replicate this measurement because it is not possible to open or extend the wings of museum specimens. In addition, we were unable to use the wing area calculation suggested by Fu et al.[55]

because wingspan measurements are not readily available for most bird species. Instead, as a proxy, we calculated the area of the 'hand' portion of both wings (hereafter termed hand-wing area, HWA) using the formula proposed in Wright et al.[66]: WL x SL x $\pi/2$ (Figure S2B). To evaluate the validity of HWA as a proxy, we compiled published estimates of the total aeronautical wing area measured from live individuals or spread-winged specimens of 755 bird species. Even though HWA accounts for a relatively small portion of the total wing area (Figure S2B), we found that HWA and total wing area are highly correlated (Pearson's correlation = 0.99; Figure S2D). This tight relationship supports the use of HWA as an index of total aeronautical wing area in our analyses and future studies. We present our full dataset of HWA for all extant bird species under two alternative taxonomic treatments – BirdTree[104] (n = 9,982 species, Dataset 1B) and Clements/eBird[115] (n = 10,657 species, Dataset 1C) – to allow integration with current and future global avian phylogenies.

Elevational distribution

To compile maximum and minimum elevation data for all extant bird species, we began by merging data from two large datasets.[100,101] When these sources lacked data for a particular species, or provided estimates that differed by >0.3 km, we filled gaps and resolved conflicts using a third dataset[99] in conjunction with other published literature. Where multiple elevational ranges were given for one species in any source (e.g. for different subspecies or localities, such as Quintero and Jetz[101]), we selected the extreme maximum and minimum values reported across the entire distribution of the species. To resolve disparities, we checked errors arising from inaccurate records or taxonomic mismatches by consulting online resources, including Birds of the World[62] and eBird data (www.ebird.org), before merging data from multiple sources and calculating the final elevation range for each species.

We applied several steps to overcome incompatibilities between data sources. First, elevation data from White and Bennett[100] are presented on a log scale, so we back-transformed data from that source and rounded to integers. Second, we omitted erroneous or uncertain estimates. For example, Quintero and Jetz[101] provided a maximum elevation of 5,895 m for Preuss's Weaver *Ploceus preussi*, a resident species restricted to lowland rainforests in West Africa under 1,000 m elevation. We revised elevational limits for all species with clearly inaccurate data. In migratory or wide-ranging species, we allowed a larger leeway for uncertainty because extralimital high- or low-elevation records are more probable. Third, we ensured that the seasonal context of elevational range data was compatible. Two core sources[99,100] provided elevation estimates from the total geographical range of each species, whereas a third source[101] provided estimates from the breeding range only. This mismatch has limited effect at the scale of our analysis because ~80% of bird species are sedentary,[65] while many migratory species reach their highest elevation during the breeding season. When we compared samples of species for which both types of data were available, we found that elevation data based on the breeding range is strongly correlated with data from the year-round range (Pearson's correlations for max elevation: 0.92, n = 7,082 species; for min elevation: 0.94, n = 6,098 species; Figures S5A and S5B). Nonetheless, to minimise inconsistency, we rechecked all migratory species with elevation data based exclusively on Quintero and Jetz[101] to ensure their maximum and minimum elevations also included data from the non-breeding season. Finally, some data inconsistency between sources arose from taxonomic mismatches, which we resolved using resources including Birds of the World[62] and Avibase (https://avibase.bsc-eoc.org/). For instance, following an older taxonomy[116] White and Bennett[100] presented a maximum elevation of 3,100 m for Freckle-breasted Thornbird *Phacellodomus striaticollis*, which has been recently split into two species with distinct elevational ranges (0-700 m for *P. striaticollis*; 1,000-3,100 m for *P. maculipectus*).[62] In such cases, we deleted erroneous data and ensured the final data agree with BirdTree[104] species delimitation used in our analyses.

After these refinements, we selected the final species-level elevation range using two alternative methods. We gave priority to the most recent estimates[99] that incorporate the latest and most complete distributional range of the species (i.e., in the order of del Hoyo[99] > White and Bennett[100] > Quintero and Jetz[101]; Method 1). This method is likely to produce more accurate estimates of minimum and maximum elevation for species, but potentially introduces subjectivity. As an alternative approach, we resampled all species by extracting the extreme minimum and maximum elevation reported for the species, with no preference for sources (Method 2). We then calculated the mean elevation for each species under both Method 1 and 2 as the midpoint between the selected maximum and minimum values; i.e., (max + min)/2. The elevation data yielded from the two methods were highly correlated for both maximum elevation (Pearson's correlation = 0.99) and mean elevation (Pearson's correlation = 0.99; Figures S5C and S5D). We therefore used our first dataset (Method 1) for all analyses. Final elevation data (Method 1 and 2) and data sources for all bird species are listed in Dataset 1B (n = 9,982 species aligned with the BirdTree phylogeny[104]). To facilitate future research, we also present elevation data (Method 1) under a modern taxonomic treatment (n = 10,657 species aligned with Clements/eBird taxonomy[115]). We converted data from BirdTree[104] to Clements/eBird taxonomy[115] via the crosswalk provided in Barber et al.[90] (see Dataset 1D for details).

Geographical and climatic data

Avian wing morphology varies with latitude,[9,117] so the effect of elevation on flight adaptation can only be understood in the context of latitudinal effects. Geographical distribution of bird species was sourced from the expert-drawn range polygons provided by BirdLife International (version 2019.1),[103] restricted to resident and breeding ranges in areas where the species is coded as extant and either native or reintroduced. Given frequent taxonomic mismatches between BirdLife and BirdTree species, we adapted the BirdLife maps using the following methods: (1) when there was a one-to-one match between BirdLife and BirdTree species (n = 8,949), we used BirdLife maps version 2019.1 for the corresponding BirdTree synonym; (2) when one BirdTree species is split into multiple BirdLife species we combined the corresponding BirdLife range polygons into a single polygon reflecting BirdTree taxonomy (n = 1,929 BirdLife splits); (3) when multiple BirdTree species share one or multiple BirdLife species ranges we used an earlier version

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of BirdLife range maps (version 2.0, published in 2012) created prior to most taxonomic changes between BirdLife and BirdTree (n = 198 BirdLife lumps. See Tobias et al.[65] for more details).

Using the adapted maps, we extracted minimum, maximum and centroid latitudes for each BirdTree species (n = 9,855 extant species with suitable maps) using R package 'PBSmapping'[109]. In contrast to AVONET[65] (which calculates both minimum and maximum latitude from the South Pole), we defined minimum and maximum latitude as the smallest and largest absolute latitudes (i.e., distance) from the equator, respectively. Species with global ranges spanning the equator therefore have minimum latitudes of 0°. To quantify the temperature seasonality experienced by each species, we first overlaid the same maps with the annual temperature seasonality (Bio4) raster from the CHELSA dataset (version 2.1)[102] at the resolution of 30 arcsecond. We then extracted the mean Bio4 value for each species by averaging grid cells that fell within the species' range using a Behrmann equal area projection, disregarding cells with less than 50% overlap. Latitude and temperature seasonality data for 9,834 bird species are provided in our final dataset (Dataset 1B).

Ecological trait data

Most previous studies describing elevational gradients in avian wing morphology (e.g. Youngflesh et al.[20]) do not account for other factors known to influence wing shape evolution, including flight mode and aerial lifestyle. Aerodynamic constraints of air density may differ between different wing uses,[30,70] so we assigned each bird species to one of the flight mode categories (flightless, flapping, soaring). Flight mode classification was based on published descriptions of flight behaviour and inspection of videos and photographs of flying birds, where available.[62] Regardless of flight mode, the extent to which species use flight also plays a major role in shaping wing morphology,[1] suggesting that elevational gradients in wing area and elongation may reflect variation in flight behaviour across different elevational ranges (Figure 1). To account for this variation, we adapted methods proposed by Weeks et al.[1] and classified each bird species according to an aerial lifestyle index, with scores ranging from 0-3 to reflect the increasing importance of flight in the daily routine of the species (0 = non-aerial; 1 = infrequent flier; 2 = moderate flier; 3 = frequent flier). Aerial lifestyle may have greater uncertainty for rare or poorly known species, so we also scored data certainty for our aerial lifestyle classifications, with certainty scores varying from A (high certainty) to C (low certainty), using methods described in Tobias et al.[91]. We present this new dataset of aerial lifestyle indices for all birds (n = 9,982 species) accompanied with data certainty estimates in Dataset 1B.

Two other factors influencing avian wing morphology – diet and habitat – are also rarely considered in studies of flight adaptation on elevation gradients. First, species occupying different trophic levels may have different foraging strategies or home range sizes, driving variation in flight behaviour.[71,72] We therefore included trophic level as a binary predictor consisting of primary consumers (herbivores and omnivores) and secondary consumers (carnivores and scavengers). Second, species living in open habitats tend to be more mobile and dispersive than those inhabiting densely vegetated habitats.[9] Thus, we used a habitat openness score in our models classifying each species as living in dense (e.g. forests), semi-open (e.g. shrublands), or open habitats (e.g. grasslands, deserts, rocky landscapes). This helps to account for the possibility that changes in wing morphology above the treeline may reflect an abrupt transition from forest species to open-country species.

Many relatively sedentary species living at high elevations in temperate-zone mountain ranges like the Alps, Rockies and Himalayas undertake winter movements over short distances (often only a few kilometres) to lower elevations.[118] This raises the possibility that higher HWI and wing area in upper elevation species simply reflects an adaptation to seasonal dispersal. In addition, long-distance migration influences wing morphology in birds, with particularly strong effects on wing-tip elongation (HWI).[9] To account for the different levels of selection pressure from short and long-distance migration, we included migratory tendency as a predictor in our models. All species were classified as either sedentary, short-distance migrants (including elevational migrants, nomadic species, and partial migrants), or long-distance migrants. Finally, raw measurements of wing morphology are correlated with body size, so we included body mass as an explanatory variable in models to assess the changes of wing elongation and area in relation to overall body size.[119] Data on trophic level, habitat openness, migratory tendency and body mass were obtained from AVONET.[65] In the case of migration data, we updated scores to emphasise elevational migrants. In AVONET, migration scores for each species are based on the migratory tendency of the largest population by geographical area, whereas in the current dataset we assign scores based on evidence for elevational migration. That is, species listed as 1 (sedentary) were switched to 2 (elevational migrants) if most high elevation populations are reported to undertake major seasonal movements downslope. Detailed descriptions of all variables are provided in Dataset 1A.

Phylogenetic data

Global bird phylogenies were downloaded from www.BirdTree.org[104] using the Hackett topology.[120] We used the full version containing all species (n = 9,993) to maximise taxonomic coverage. From 10,000 trees provided, we randomly selected 100 trees and used this subset in all phylogenetic analyses.

METHOD DETAILS

After removing flightless, invalid and extinct taxa, our sample contained 9,937 extant bird species. To assess the relationship between elevation and wing morphology while accounting for evolutionary relatedness among species, we used phylogenetic generalised least square (PGLS) models implemented with the R package 'phylolm'[111]. Our main models test whether interspecific variation in a flight-related morphological trait (HWI or HWA) can be predicted by the maximum elevation reached by each species. We

used maximum elevation as our main predictor because the air density gradient is likely to constrain flight performance most acutely at the uppermost elevations. The value of maximum elevation per species also suffers from less ambiguity than other metrics such as mean or median elevation, given the largely unknown population distribution of most species. To further explore the details of wing morphological changes, we modelled wing length and width changes using WL and SL as the response variable.

QUANTIFICATION AND STATISTICAL ANALYSES

All statistical analyses and visualisation were implemented in R[105] version 4.2.2.

Phylogenetic modelling

Multivariate PGLS models were used to account for the effects of alternative explanatory variables, including elevation and eight additional environmental and ecological predictors: centroid latitude, temperature seasonality, habitat openness, body mass, flight mode, aerial lifestyle, migration and trophic level. Latitude was calculated from the centroid of the breeding range (i.e., wherever the species is known to breed, including the resident range). Detailed definitions of all variables used in this study are presented in Dataset 1A. We also added an interaction term between elevation and flight mode because in flapping flight and soaring flight, lift is generated through different mechanisms at different energetic costs to the bird,[30,70] and therefore flight mode may induce divergent aerodynamic effects at the same air density. To assess the absolute change of wing morphology with elevation, we repeated models with body mass removed from explanatory variables. To disentangle the elevational gradient of wing morphology from that of overall body size, we ran PGLS models using body mass as the response variable, and all the remaining predictors as the explanatory variables.

In each analysis, we accounted for phylogenetic uncertainty by running models 100 times using the same set of randomly selected trees. We then averaged parameter estimates using Rubin's rules as recommended by Nakagawa and De Villemereuil,[121] implemented with the R package 'mice'[112]. To account for allometric scaling,[122] we log-transformed morphometric values, including body mass, wing area and other linear measurements (WL, SL). We also log-transformed temperature seasonality, and square root-transformed elevation and centroid latitude to normalise the data distribution. The remaining variables are ordinal (habitat openness, aerial lifestyle, and migration) or categorical (flight mode and trophic level) and were untransformed following previous studies.[91] We scaled all continuous variables to a mean of zero and standard deviation of 0.5 to facilitate direct comparison between the effect sizes of continuous and categorical variables.[123] Response variables were also scaled to enable comparison between wing morphological metrics. Collinearity between explanatory variables was low to moderate (variance inflation factor: 1.02–4.18), with the highest correlation found between centroid latitude and temperature seasonality. We also assessed model fit with conditional R^2 values calculated using the R package 'rr2' which accounts for the hierarchical data structure.[124] We report any results where the 95% confidence intervals do not span zero as statistically significant.

To examine finer-scale and potentially non-linear responses of wing morphology to elevation (Figure 2), we used a 'sliding window' approach where species were assigned to a series of 3-km wide elevational bands according to their maximum elevation. The lowest band starts at sea-level, with each subsequent band starting 1 km higher than the previous one (i.e., the first band spans from 0-3 km, the second band from 1-4 km, and so on, up to the highest band of 5-8 km). Note that bands are overlapping so a species may be assigned to multiple bands. For example, a species reported up to a maximum elevation of 1 km would appear in the first and second bands. Only one species - Alpine Chough *Pyrrhocorax graculus* – occurred at a maximum elevation above 8 km, so we included this species in the highest band. We then ran independent models within each of the six elevational bands using the same set of predictors. Continuous environmental predictors were re-standardised from original values within each elevational band (instead of across the entire data distribution as used in the main global models) to ensure their effect sizes are comparable across bands.

It is possible that using maximum elevation to divide elevational bands is misleading because higher elevational bands may contain a greater proportion of species that largely occur at lower elevations, increasing the likelihood of mismatches between elevational band assignment and the elevation at which measured specimens were obtained. For example, the Common Raven *Corvus corax* has a maximum reported elevation > 6 km above sea-level while also occurring widely in lowlands. However, this is unlikely to have substantial impact on our band assignment since globally 93.8% of species have an elevation range less than 3-km wide (discounting long-distance migrants). To assess how the breadth of elevational ranges varies across the elevational bands, we plotted maximum, mean and minimum elevations calculated for all non-migratory species assigned to each band (Figure S6). We found that as maximum elevation increases, the mean and minimum elevation similarly increase. Therefore, while the individual specimens measured in our dataset may have lived below the elevational band to which they are assigned, most montane species have relatively narrow elevational ranges and thus the samples used in Figure 3 reflect the likelihood of adaptation to high elevations.

Within-family comparisons

Some non-migratory bird species found at high latitudes have evolved adaptations for more efficient dispersal to avoid harsh climatic conditions, even at low elevations where air thinness is irrelevant (Figure 3C). It is therefore necessary to test whether the longer wings of montane species are under selection for mobility via climatic mechanisms rather than thin air alone. Our PGLS models help to rule out this possibility by quantifying the effect of elevation while statistically holding all other factors constant, including long-distance migration, altitudinal migration, aerial lifestyles and occurrence in more open habitats. To provide further evidence, we also conducted within-family comparisons. Specifically, we compared species living at high latitudes (minimum latitude > 30) and low elevation (maximum elevation < 3 km) against members of the same family living at high elevation (maximum latitude < 30) and low latitudes

(maximum elevation > 4 km). After removing long-distance migrants, 14 families had a minimum of three species in each sample. For each of these families, we used a paired t-test to assess whether the median HWI or HWA was statistically different between the two categories. Note that these tests are not phylogenetically controlled as the matched comparisons within families already broadly control for evolutionary relatedness. Family assignments followed the Clements/eBird checklist.[115]

Sensitivity analyses

To examine potential biases in our dataset, we ran sensitivity analyses with marine species and long-distance migrants removed. Marine species (seabirds) are potentially anomalous because many of them specialise in 'dynamic soaring', a flight style that generates lift from the gradient of wind speed.[73] This contrasts with terrestrial soaring species, most of which use 'thermal soaring' to generate lift from thermal convection currents.[52] Another problem relating to marine species (including non-soaring species) is that a key predictor, temperature seasonality, is based on land surface temperature and therefore the data is less accurate for seabirds. The reason for removing long-distance migrants relates to uncertainty about the elevations used on their migratory flightpaths. Some migrants fly at extreme altitudes during migratory journeys, yet estimates are available for only a handful of species with sufficient tracking data.[74,75] Anecdotal observations of migratory birds are often made well above their normal elevational ranges, but it is not clear whether these events reflect ecological conditions relevant to selection on flight efficiency. For example, the Steppe Eagle *Aquila nipalensis* regularly occurs up to 2.3 km above sea-level during the breeding season,[101] and sometimes higher on migration, with one migrant observed crossing the Himalayas at 7.9 km above sea-level.[98] This raises the question of whether to assign the species a maximum elevation of 2.3 km, to reflect typical elevational limits, or 7.9 km, which could either be viewed as an accurate reflection of physiological limits, or a rare event exaggerating the strength of adaptation to thin air. Regardless of the view adopted, the uncertainty in elevational data is higher for migrants than residents, with an increased discrepancy between different data sources (Figures S5A and S5B). To assess whether our results are affected by the inclusion of seabirds and long-distance migrants, we ran an initial sensitivity analysis focused on non-migratory landbirds only (n = 8,703 species; throughout this article, we use the term 'non-migratory' as shorthand to refer to sedentary species and short-distance migrants).

To further test the robustness of our results, we ran two additional analyses, one excluding species with uncertain flight behaviour from models, and another using mean elevation instead of maximum elevation as the response variable. Since the likelihood of assigning incorrect aerial lifestyle is increased in poorly known species, we repeated models while only retaining species with the highest-certainty aerial lifestyle data (certainty score = A; n = 6,854 species) to assess the effect of data uncertainty. In the other analysis, we replaced maximum elevation with mean elevation because maximum elevation data are more sensitive to sampling effort and sometimes reflect extreme or unusual observations, while mean elevation may reflect the more typical air density experienced by the species. In addition, when running the second sensitivity analysis for our 'sliding-window' models, we also re-assigned species to elevational bands based on their mean elevation instead of maximum elevation in congruence with the model structure (i.e. mean elevation as the response variable).

We also explored the effect of our methods used to divide elevational bands in our final analyses. The results reported in Figure 4 are based on a bandwidth of 3 km, which was selected as a compromise between precision and sample size - smaller bandwidths tend to under-sample the variation within the band; larger bandwidths provide less detail about variation across the elevational bands. To assess whether our results are robust to variation in bandwidth, we re-ran our models using bandwidths set to 2 km and 4 km.